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Biology of horse nettle, *Solanum carolinense* L

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BIOLOGY OF HORSE NETTLE
SOLANUM CAROLINENSE L.

by

Erhardt P. Sylwester

A Thesis Submitted to the Graduate Faculty
for the Degree of
DOCTOR OF PHILOSOPHY

Major Subject: Plant Morphology

Approved:

Signature was redacted for privacy.

In Charge of Major Work

Signature was redacted for privacy.

Head of Major Department

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Iowa State College
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INTRODUCTION

Weeds are recognized to be one of the major hazards of crop production. Weeds compete with crop plants for light, water and nutrients, and are thereby responsible for serious crop losses, as well as for the substantial expenditures of time, labor and materials necessary for weed control. Some qualities that enable weeds to assume this important role are their aggressiveness, persistence when established, copious seed production, long-lived seeds, means of wide dissemination, tolerance to severities of climate and adaptability to a variety of soils. The losses have been conservatively estimated to be at least fifty million dollars annually in Iowa and three billion dollars annually for the nation. These losses are exceeded only by the loss caused by soil erosion.

The Iowa weed law designates seventeen weeds as noxious. The list is divided into eight primary and nine secondary noxious weeds, in accordance with their relative importance. The eight primary noxious weeds are distributed in six families and the nine secondary noxious weeds in seven families.

The control of a weed is facilitated by an understanding of its growth habits, reproduction, natural enemies, and other aspects of the biology of the plant. Some of the primary noxious weeds have been studied in detail by previous investigators. The biology of one of our most serious weeds, Solanum

carolinense L., the horse nettle, the subject of this study, has not been studied intensively heretofore.

Horse nettle is an herbaceous perennial member of the Solanaceae. It is known by such local names as bull nettle, apple of Sodom, devil's potato, devil's tomato, wild tomato, sandbriar, radical-weed, tread-softly and Carolina nightshade. The plant is classified by the Iowa Weed Law as a primary noxious weed. It is the only primary noxious weed of Iowa which is a native of the United States, but it is not native to Iowa. Horse nettle occurs most frequently and extensively in southern Iowa, but it has progressed northward slowly and is now found in many of our most northern counties.

Horse nettle is objectionable on any type of land, but it becomes especially serious in cultivated fields, pastures and meadows. It also becomes a pest along roadsides, railroad tracks and ditchbanks. Although horse nettle does not take complete possession of cultivated land, it reduces the quality and yield of crops, adds to the difficulty of farming operations, and lowers the value of land. Most animals avoid the plant, probably because of its spines and unpalatability. Grass usually remains untouched near horse nettle plants unless other forage is scarce, thereby resulting in much grazing loss in heavily infested pastures.

The present investigation of the life history of the horse nettle has emphasized the developmental morphology of the plant, its distribution, growth, flowering, fruiting, and the dissemination and germination of seed. Practical experiments were conducted on the control of this weed by means of chemicals and cultural methods.

REVIEW OF PERTINENT LITERATURE

The Solanaceae and the genus *Solanum* figure prominently in the botanical writings of the 19th century, especially in treatises on medicinal and poisonous herbs and on plant classification. Many members of the family were known and utilized by the ancients. Some writings of Plutarch probably referred to members of this family. One of the earliest references is that of Gerard, whose rewritten Herbal was published by Woodward (117). Early references to the medicinal and poisonous nature of the Solanaceae were made by Winkler (113), Berge and Riecke (14), Charles Johnson (59) and Laurence Johnson (60). Huseman, Hilger and Huseman (56) stated that solanine was discovered by Defosses in 1820 in the berries of *Solanum nigrum* L. and *Solanum dulcamara* L. The authors gave the chemical formula of solanine and described the method of extraction. Other references to the medicinal or

poisonous properties of the Solanaceae are those of Millspaugh (73), Chesnut (20), Koehler (70), Halsted (49), Henslow (55), Kraemer (71), Walsh (109), Kanngiesser (62), Ellis (38), Thompson and Sifton (105), Stevens (97), Steyn (101), and Gress (48). Horse nettle was stated to be medicinal or poisonous by Schaeffner (90), Detmars (35), Pammel (79), Kellogg (64), Garman (40), Youngken (118), Sievers (91), Gates (41), Hanson (51), Muenscher (75), and Muenscher and Winne (76).

The nightshade family contains approximately 75 genera and nearly 2,000 species of very wide distribution. The members are most abundant in the tropics, but the family is well represented in temperate regions. In addition to poisonous members, the family contains numerous food plants, ornamentals, and weeds. Some common Solanaceous weeds are: Jimson weed, Datura stramonium L.; perennial groundcherry, Physalis heterophylla Nees and Physalis subglabrata Mack and Bush; buffalo bur, Solanum rostratum Dunal; white horse nettle, Solanum elaeagnifolium Cav.; horse nettle, Solanum carolinense L.; melon-leaved nightshade, Solanum triflorum Nutt and many others. In addition there are such weedy poisonous plants as deadly nightshade, Atropa belladonna L.; bittersweet, Solanum dulcamara L.; black nightshade, Solanum nigrum L.; henbane, Hyoscyamus niger L.; Jimson weed, Datura stramonium and many others.

The genus Solanum contains nearly 1,200 species of wide geographic distribution. The name of the genus is derived from the Latin term "solamen", referring to the sedative

qualities of the drugs obtained from many plants of this genus. The genus *Solanum* presents a diversity of forms including herbs, shrubs and small trees. Many cultivated species are familiar agricultural and horticultural plants.

Gray (46) lists eight species and one variety of *Solanum*. Britton and Brown (17) list twelve species and state that some twenty others occur in the southern, western and southwestern part of the United States. Bailey (4) lists eighteen species and Rydberg (89) lists eleven species. From the above diversity of classification it is apparent that the genus requires further study. Horse nettle, *Solanum carolinense* L. was first classified by Linneaus in his *Species Plantarum* 184 in 1753. This original classification is still in use.

Anatomical work on members of the Solanaceae occurs widely scattered in the literature. According to Woodcock (114), Hanstein was the first to describe sieve tubes in the Solanaceae, and Peterson (86) discussed the relative amount and distribution of external and internal phloem in several genera. Collin (21) made some anatomical studies of deadly nightshade and Jimson weed. Artschwager (3) described the gross morphology, anatomy and ontogeny of stem, leaf, root, stolons, tuber and flower of potato. Cooper (22) described the morphology and anatomy of the tomato inflorescence. Working with diploid (N-24) and triploid (N-36) plants of tomato, Jorgensen (61), found that the leaves of diploid plants were larger, the number of

leaflets was fewer, the primary leaflets were much broader and the leaf was thick and deep green. Triploids were more hairy than diploids. No observations were made on haploid plants. Jorgensen also made chromosome counts of a large number of species in the Solanaceae, including Solanum dulcamara (n-12) Solanum tuberosum (n-24) and Solanum nigrum (n-36). There is obvious polyploidy in the Solanaceae.

King (69) found that the root-stem transition of the tomato is similar to that of the potato. Smith (93) made a morphological study of the Bonnie Best tomato, including the development of the flower, sporogenesis, gametogenesis, fertilization, and the development of the embryo, endosperm and fruit. The study was undertaken to determine the morphological basis of "blossom drop". Woodcock (114)(115)(116) described some histological and anatomical features of haploid and diploid tomatoes. Hayward (53) presents the most recent and complete summary of the anatomy of the tomato and potato.

Four of Iowa's noxious weeds have been investigated anatomically. Stevens (95) studied sow thistle in some detail. Kennedy and Crafts (65) studied the growth habits and anatomy of field bindweed, Convolvulus arvensis. Kiesselbach, Peterson and Burr (66) conducted a similar study of the same plant. Bakke (5,6) described some anatomical features of leafy spurge, Euphorbia esula, in addition to

summarizing knowledge of the origin, distribution, life history and eradication of the plant. Simonds (92) studied perennial peppergrass, Lepidium draba.

The anatomy of horse nettle has received very little attention. Pammel and Fogel (82) described briefly the underground organs. They state that it is difficult to distinguish horse nettle root from underground stem except by microscopical examination. They also state that during the winter the stem dies back to near its origin in the root. Pammel and Dox (81) found that the seeds contain abundant protein but no starch.

Literature dealing with weed control is voluminous, principally in the form of popular bulletins, leaflets and pamphlets. Some technical books and research publications are also available. This brief review will be limited to the most pertinent and recent material concerning the eradication of horse nettle and of some other pernicious weeds which present similar problems.

Specific control methods have been crystallized and put into writing since about 1900. Pammel et al (83, 84), Gress (47), and Runnels and Schaffner (88) advocated the control of horse nettle by clean cultivation and by the use of smother crops. Muenscher (74) proposed the use of chemicals and clean cultivation. Wilson et al (112) recommended the use of chemicals for the control of small areas and cultural control methods for the larger infestations. Kinch (68) advocated

the use of chemicals as well as smother crops for the control of horse nettle. Burlison et al (19) proposed clean cultivation and fallow cultivation for large heavily infested areas and chemical control methods for smaller infestations. Essentially the same methods were recommended by Darlington et al (33), Lee (72), Gates (42), Drew and Helm (37), James and Alexander (58), and Sylwester and Porter (103).

Control by cultural practices has been widely recommended for weeds other than horse nettle. The principal practices are crop rotation, clean cultivation, fallowing and smother crops. Such methods, singly or in combination are stated to be effective in controlling perennial sow thistle (95), Canada thistle (36), quack grass (102), bindweed (66) (119) (8) (67) (99) (108) (63) (7) (9), leafy spurge (12) (52) (6), Russian knapweed and perennial peppergrass (54).

Weed seed production was extensively studied by Stevens (96) and weed seed viability and germination by Darlington (32) and Brown and Porter (18).

The relationship of root reserves to weed eradication was studied by Army (1) and by Bakke, Gaessler and Loomis (9). Crafts (24) (25) (26) (27) (28) (29) and Crafts et al (30) (31) have compared the unique killing action and residual effects of sodium chlorate, sodium arsenite, boron and thallium sulfate, and also studied the effectiveness of arsenical sprays for the control of deep-rooted perennial weeds.

Ball and French (10) studied the control of annual weeds by means of sulfuric acid. Westgate and Raynor (111) described the control of certain annual weeds by means of Sinox, a new selective spray. Boyd and Corkins (16) worked with weed burners and found that three light burnings per year for three years eradicated most noxious weeds under Wyoming conditions.

Numerous useful weed bulletins are available, dealing with identification and practical control methods. Some of the best known bulletins are by: Pammel et al (83), Gress (47), Haney (50), Runnells and Schaffner (88), Ball et al (11), Tehon (104), Jackman et al (57), Benson (13), Wilson et al (112), Kinch (68), Cox (23), Burlison et al (19), Boyd and Corkins (15), Lee (72), Darlington et al (33), Stevens (98), Thornton and Durrell (106), Gates (42), Drew and Helm (37), Neatby (77), James and Alexander (58), and Sylwester and Porter (103).

Several reference texts are also available on this subject. Among older books are those by Pammel et al (84) and Georgia (43). Muenscher's recent text (74) is adapted to the needs of laymen, teachers of vocational agriculture, county agents and others engaged in agricultural pursuits. Robbins, Crafts and Raynor (87) is also suitable for general use, though much more technical than the preceding book. These recent texts contain useful bibliographies.

MATERIALS AND METHODS

Material for histological study was secured primarily from plants in the field in Story county, Iowa. Collections were made throughout the course of the study from 1937 to 1944. Seeds were taken from plants in the field, the berries were crushed, the seeds washed in several changes of water, dried at room temperature and stored. Seedlings were secured by germinating the seeds between moist blotting paper in a seed germinator at 35°C.

Three killing fluids were used, F.A.A., Bouins fluid and a Nawaschin (Craf) formula (1% chromic acid, 20 cc.; 1% acetic acid, 75 c.c.; 35% formaldehyde, 5 c.c.). The last formula was used most extensively. Although an interval of 24-48 hours is sufficient for killing and fixing, the material was usually left in the killing-fixing solution for much longer periods.

All histological material was dehydrated in an acetone-normal butyl alcohol series, or in a dioxan series, and imbedded in paraffin. Mounted blocks of the tougher imbedded material were soaked in warm water (35° C.) for 24 hours. This procedure facilitated sectioning. Sections were stained in hemalum-safranin, or safranin-fastgreen.

All field observations, cultural studies and eradication experiments were performed in the vicinity of Ames, Story

county, Iowa, except as otherwise noted. Specific methods used in seed germination are described in conjunction with the germination studies.

EXPERIMENTAL RESULTS

Distribution of Horse Nettle

The following data were assembled by examination of herbarium specimens, by correspondence and by observations throughout Iowa.

Horse nettle occurs from southern Ontario, Vermont, Massachusetts and Florida, westward and southwestward to Illinois, Nebraska, Kansas and Texas, being adventive north-eastward and westward (46, 17, 89, 107, 43, 94). It is indigeneous to the southern states (84, 74, 75, 85, 78, 34, 100, 112), from where it has been introduced northward and westward. Specimens in the herbarium of Iowa State College include plants from New York, District of Columbia, Pennsylvania, West Virginia, North Carolina, South Carolina, Georgia, Louisiana, Alabama, Ohio, Texas, Oklahoma, Missouri, Nebraska, Iowa, Illinois, and Minnesota. Correspondence by the author with State Agricultural Departments of all the states indicates that horse nettle is found in all states except Wyoming,

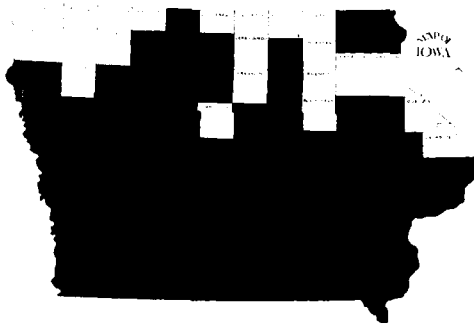
Colorado, New Mexico, Arizona, Nevada, Oregon, Washington, Montana, North Dakota, Maine and New Hampshire. It was listed as a noxious weed in Ohio, Michigan, Indiana, Illinois, Minnesota, Wisconsin, Iowa, Nebraska, Kansas, Missouri, Kentucky, and Texas as early as 1911 (80). In 1939 horse nettle was declared noxious by the weed laws of seven states and noxious in the seed laws of eleven states. The number of states declaring this weed noxious in their weed and seed laws has increased since 1939.

Horse nettle is adventive in Iowa. Specimens in the herbarium at Iowa State College date back to 1890. The plant was first recorded for Story county by Stewart and by Sirine. Collections were made in Story county by Pammel and again by Rolfe in 1891; in 1895 by Fitzpatrick in Decatur county and Fuller in Clinton county; in 1896 by Fitzpatrick in Des Moines county and Ball in Story county. Thus, before the turn of the century, horse nettle was present in Iowa at least as far north as Clinton and Story counties.

In the Iowa State College herbarium there are 72 specimens which have been collected in Iowa since 1900. The counties and dates of collection follow:

Allamakee	-- 1902, 1922, 1923, 1925	Johnson	-- 1920
Boone	-- 1914, 1924, 1928	Jones	-- 1928
Buchanan	-- 1926	Keokuk	-- 1903
Buena Vista	-- 1918, 1922, 1923, 1925, 1929	Lee	-- 1931
Calhoun	-- 1922, 1924	Linn	-- 1918
Carroll	-- 1906, 1929	Mahaska	-- 1928
Clarke	-- 1906	Monona	-- 1929
Clayton	-- 1929	Palo Alto	-- 1922
Dallas	-- 1902	Plymouth	-- 1923
Davis	-- 1927	Pocahontas	-- 1906, 1921
Decatur	-- 1905	Polk	-- 1924, 1927
Delaware	-- 1922	Sac	-- 1922, 1924
Des Moines	-- 1930	Scott	-- 1925
Fremont	-- 1925	Shelby	-- 1913
Greene	-- 1902, 1906, 1922, 1929	Story	-- 1909, 1927
Grundy	-- 1904, 1922	Taylor	-- 1927
Guthrie	-- 1904, 1925, 1928	Union	-- 1902
Hancock	-- 1903	Wapello	-- 1903
Hardin	-- 1923	Warren	-- 1924
Humboldt	-- 1921, 1929	Winnebago	-- 1920
Ida	-- 1923	Woodbury	-- 1919
Jasper	-- 1922	Wright	-- 1926, 1930

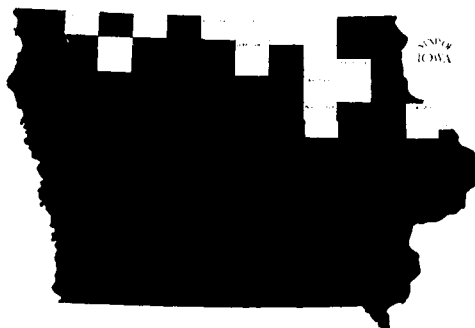
DISTRIBUTION OF HORSE NETTLE IN IOWA 1926 - 1945



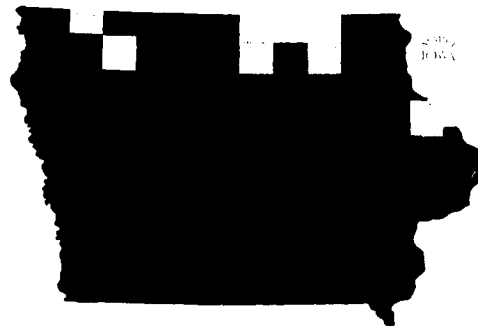
1926-77 COUNTIES



1935-82 COUNTIES



1940-86 COUNTIES



1944-91 COUNTIES



1945-94 COUNTIES

PLATE I

Horse nettle was found in 70 Iowa counties in 1926 (84). A check of herbarium specimens adds seven counties, making a total of 77 in 1926. By 1935 the plant had been reported from 82 counties; by 1940 from 86 counties, and since 1940 the number of counties reporting this plant has risen to 94. The plant is much more serious as a weed in southern than in northern Iowa. Only five counties in Iowa have not reported the plant. The spread of the plant from 1926 to 1945 is shown in Plate I on page 14. Horse nettle was found in 77 counties in 1926. At the present time it is found in 94 counties. The approximate probable date of introduction of horse nettle into Iowa was about 1866 (84).

Description of the Plant

Horse nettle is a perennial, erect, branched, stout, herbaceous plant, ranging in height from six inches to two feet (Figs. 1, 2). The largest horse nettle plant observed was forty inches high. All aerial parts of the plant, except anthers and pistil, bear many minute, short stiff 4-8 rayed hairs and also numerous capitate hairs. As the season advances the hairs tend to slough off, though many remain throughout the season. The main stem of the plant is loosely branched at the top. The stems, petioles, leaves, racemes, peduncles and calyx bear numerous short, smooth, stout, awl-shaped yellowish

prickles (Fig. 2). The leaves are simple, alternate, oblong or ovate. The margins vary from sinuately toothed to irregularly and deeply lobed or cut. Some variations in the leaves are shown in Figure 3.

Rhizomatous stems arise from vertical as well as from horizontal roots, either from undisturbed roots or from root fragments resulting from cultivation. Under favorable conditions, pieces of rhizome can also become established. Thus horse nettle is able to spread vegetatively by both underground stems and roots. Both aerial and underground stems callus readily. Rhizomes bear numerous, small lateral secondary adventitious roots and lack the chlorophyll and spines which characterize aerial stems.

The perennial roots of horse nettle attain a depth of 7-11 feet. Plants grown from seed planted in the spring develop a vertical root system which varies from 18-36 inches in depth at the end of one growing season (Figs. 4, 10, 11). The tortuous roots frequently exceed a diameter of $\frac{1}{4}$ inch. These large roots have many small lateral roots. The horizontal root system, which is always less extensive than the vertical root system, is initiated in the second year of growth and is normally found at depths of 6-12 inches (Fig. 7). Macroscopically the horizontal roots resemble vertical roots.

Flowering is continuous and abundant in the vicinity of Ames from the first part of June to the latter part of August.

Acetocarmine smears disclosed flowers in meiosis September 1, September 20 and October 14, 1941. In 1941 plants were still blooming in the vicinity of Ames on October 15. Floral and vegetative development continues to some extent until frost. The anthers shed pollen the first day after the flower opens. Pollen is shed from an individual flower for about four days and on a raceme for an average period of about 15.2 days (Table 1).

Flowers are borne on prickly pedicels in loose clusters or in simple cymose racemes. The racemes appear to be terminal at first but are actually lateral, as is evident during the fruiting stage (Fig. 1). The mature pedicels range in length from .6 - 1.5 centimeters, the average of 100 measurements being 1.08 cm. The pedicels are recurved when in fruit (Fig. 1). The flowers open in the morning, remain open throughout the day and close loosely at night. The individual flowers normally last about four days. The flowers begin to wither on the fourth day and gradually turn brown on about the fifth day, the petals usually shrivel and the flower no longer opens. The highest number of macroscopic buds observed upon a single raceme during the study was 23, ranging in size from fully opened flowers to very minute buds. The average number of macroscopic flower buds per raceme usually varies from 4-20, the average of 100 observations being 9.64 macroscopic buds. It is very common to see as many as

two or three flowers open on a raceme at one time, five being the maximum number observed on a single raceme at one time. The length of time required for an entire raceme to complete flowering is shown by the following data collected during the 1938, 1939 and 1940 seasons (Table 1).

Table 1
Blooming of Horse Nettle

Year	First Flowers on Raceme Open	Last Flowers on Raceme Finish Blooming	Number of Flowers	Time Elapsed (days)
1938	June 27	July 14	11	17
	" 27	" 15	8	18
	July 8	July 22	9	14
	July 16	July 29	11	13
1939	June 11	June 26	11	15
	July 10	July 23	7	13
	July 15	July 28	8	13
	July 20	Aug. 5	10	16
1940	June 28	July 16	11	18
	June 30	July 19	9	19
	July 12	July 26	9	14
	July 14	July 27	7	13
	July 15	July 30	8	15
	July 16	July 30	9	14
	July 16	August 2	11	17
Average			9.26	15.26

The flower of horse nettle resembles that of potato. The calyx is 5-lobed, and the tapering calyx lobes are about one-half of the length of the corolla. The calyx is rotate, persistent and united at the base of the fruit. The corolla is wheel-shaped or rotate, 5-lobed and plicate. The color of the corolla ranges from white to pale violet or light purple. The diameter of the corolla when fully expanded varies from 1.5 - 3 cm. in width, the average width of 100 corollas being 2.78 centimeters. The five stamens are adnate to the throat of the corolla. The anthers are elongated and narrow and converge at their tips, forming a loose cone. The anther sacs open by means of terminal pores. The single ovary has an elongated, 2-lobed stigma.

The ovary is most commonly two celled. The fruit is a spherical berry in a persistent calyx. The berry resembles a small tomato. It is green at first, and becomes brilliant yellow, orange-yellow or brownish after frost or upon maturity. The mature fruits range from $\frac{1}{2}$ centimeter to 2.4 centimeters in diameter. Measurement of 100 berries collected at random gave an approximate average berry diameter of 1.5 cm. The mature berries resemble those of groundcherries which have had their husks removed. The smooth skin of the berry is very thick and waxy. The berry is filled with a very juicy pulp and many seeds. The berries lose approximately 81.5 per cent water when air dried (Table 2).

Table 2

The Water Content of Horse Nettle Berries,
Collected at Ames, October 3, 1936.

No. of Berries per lot	Green Weight of Mature Berries in Grams	Air Dry Weight of Mature Berries in Grams	Air Dry Weight of Seed in Grams	Moisture Lost in Grams	Percent Water Lost
50	22.5	4.5	1.5	18	80.0
50	23.4	4.7	1.7	18.7	79.9
50	66.7	12.4	4.7	54.3	81.4
50	69.9	12.6	4.8	57.3	81.9
50	112.7	19.5	8.1	93.2	82.6
50	126.2	20.6	8.3	105.6	83.6
Average					81.5

A count of 100 racemes showed that the number of berries per raceme ranged from 1 to 9, the average being 5.1 berries per raceme. It is not uncommon to find as many as 10-15 racemes upon a single plant, the highest number observed being 17. The highest number of berries observed upon a single plant was 144. The usual number, however, is much smaller. A count of 500 plants gave a range from 3 to 111 berries per plant, and an average of 24.9. The ripening berries gradually shrivel and mummify and frequently remain on the defoliated plant throughout the entire winter. Seeds are liberated by the disintegration of the berry.

The seeds of horse nettle are rounded, ovate or obovate, very much flattened laterally, glossy, granular, or reticulate, yellow to light orange or light brown. The seeds resemble those of groundcherries (*Physalis* spp.) and are distinguished from them only with difficulty. Usually horse nettle seeds are somewhat larger than groundcherry seeds. The average length of 100 seeds taken at random was 2.28 millimeters and the average width 1.87 millimeters. Six random lots, each containing 100 air dried seeds gave an average weight of .16 milligram per seed.

Seed is produced in great abundance if the plants are not cut often. Mature seed, as evidenced by germination tests, is usually produced by the middle of August in the vicinity of Ames. The earliest germination recorded during the course of this study was from berries picked August 1, 1941. Seed production is continuous at Ames until the end of the growing season. Fifty flowers, which were marked when the first blossoms opened, required an average of 40 days to mature seed. The average number of seeds borne per berry is given in Table 3.

Table 3
Relation of Berry Size to Weight of Berries,
Weight and Number of Seeds Produced.

	Diameter of berries in centimeters		
	$\frac{1}{2}$ - 1	1 - $1\frac{1}{2}$	$1\frac{1}{2}$ - 2
Total green weight of 100 berries (grams)	45.1	142.8	219.0
Total number of seeds per 100 berries	1383	5225	8701
Average number of seeds in each of 100 berries	13.83	52.25	87.01
Total weight of air dry seed of 100 berries (grams)	1.63	9.62	16.53
Total weight of 500 air dry seeds (grams)	.6873	.9510	.9330
Average weight per seed in relation to berry size (mg.)	1.3	1.9	1.8

From Table 3 it is apparent that much variation exists in the number of seeds produced per berry as well as in the weight of seeds produced in different sized berries. In general, the number of seeds produced, and the weight of the seed produced, is directly proportional to the size of the berry. The weight per seed is directly proportional to the size of the berry, however, the maximum weight is reached in berries ranging from 1 - $1\frac{1}{2}$ cm.

Histology of Vegetative Organs

Development and structure of the leaf

Shoots arising from perennial rootstocks were consistently found to have seven macroscopic leaves at the time of emergence from the ground. Sections of these shoots were used to ascertain the structure of the promeristem and the method of leaf initiation. The tunica of the promeristem consists of a single layer of cells characterized by anticlinal cell walls. The inner zone or corpus is a homogeneous region in which the planes of cell division have no consistent orientation. Leaf formation is initiated in the corpus, involving at least three layers of cells. Accelerated cell division produces a leaf primordium as a lateral protuberance on the promeristem. The young leaf primordium is at first a flattened cylinder in cross section. The marginal meristem is initiated by a series of cell divisions occurring simultaneously on the lateral edges. The lamina of the leaf is derived by further activity of the marginal meristems (Figs. 17-23).

Differentiation into distinct palisade and spongy parenchyma is distinguishable in the second leaf from the apex. The epidermal cells become uniform and regular in size and outline. The layer of isodimetric cells adjacent to the upper epidermis differentiates into a compact palisade tissue by elongation, whereby the cells attain twice their original

vertical dimension. The spongy parenchyma is stratified in the second leaf, and this stratification and the approximate isodiametric size persist even after the zone has become distinctly spongy. Intercellular spaces become prominent in the fifth leaf and marked elongation of palisade is evident in the sixth leaf. All non-vascular tissues are fully delimited in the third leaf. Subsequent development of the leaf consists primarily of expansion and differentiation of these tissues and the differentiation of vascular tissues (Figs. 17-23).

Procambial cells can be recognized in the first leaf, 80 μ below the tip. The procambial cells occur as small concentric groups surrounded by the larger cells of the ground parenchyma. In the leaf primordium the first vascular elements arise in the median bundle. Phloem and xylem elements are differentiated more or less simultaneously. Protophloem and spiral protoxylem elements are distinguishable 150 μ from the end of a strand. The groups of thin-walled phloem initials are arranged in the form of a crescent on the abaxial = dorsal, (outer or lower) side of the leaf, with the concave side of the crescent toward the axis of the plant. As differentiation takes place, procambial cells between the xylem and outer phloem undergo cambiform division and the derivatives give rise to secondary vascular elements. The mature midrib usually exhibits 8-10 groups of outer phloem and 6-8 groups of inner phloem, separated by parenchymatous cells of irregular size. Secondary vascular elements consist largely of sieve tubes,

companion cells and annular xylem elements. The small tributary veins resemble the main vein in all respects except in the number and size of phloem and xylem elements.

The lamina of the mature leaf consists of approximately seven layers of cells (Fig. 24). A thin layer of cuticle covers both surfaces of the leaf. The upper epidermis is a single layer of closely fitting cells. Adjacent to the upper epidermis, a single row of closely fitting, chlorophyll-bearing palisade cells forms a compact tissue. The zone of spongy parenchyma is approximately four cells in thickness and contains chlorophyll. The lower epidermis consists of a single row of cells. Stomata are more numerous on the lower surface. The mid-vein is crescent shaped in outline. The phloem strands on the dorsal side of the bundle consist of sieve tubes, companion cells and phloem parenchyma. The cambium consists of a stratified zone of elongated, closely fitting cells. The xylem consists of lignified annular and scalariform vessels and xylem parenchyma. A few phloem strands are also found on the ventral surface of the vein. Branch veins resemble the midvein except for size.

Development of hairs and prickles

Stellate and capitate hairs are present in large numbers very early in the ontogeny of all above-ground portions except stamens and pistils. The short stalked capitate or glandular

hairs arise first and are derived from epidermal cells (Fig. 25). An epidermal cell becomes bulged and undergoes periclinal division. The inner daughter cell becomes the stalk cell, and subsequent division of the outer cell gives rise to a 4-6 celled capitate hair. The nucleus in all cells is large and the cytoplasm is very dense. The stellate hairs, which arise later and attain macroscopic size, also arise from the epidermis. The first cell division is periclinal. The derivatives of subsequent divisions produce the bulbous base and four or five tapering one-celled points (Fig. 26). The epidermal cells at the base of the hairs form a distinct raised area. The cells of stellate hairs become vacuolate and the matured walls exhibit striations (Fig. 27). The stellate hairs are durable, retaining their shape on dead plants in the field for more than a year.

Many parts of the horse nettle plant are beset with numerous yellow, sharp, stiff prickles which attain a length of 5-6 mm. Early in the ontogeny of the plant these prickles arise as protuberances by anticlinal and periclinal divisions of the epidermis and outer cortical region. The cells of the protuberance enlarge and elongate. The epidermal and collenchyma cells grade into the elongated sclerified cells of the protuberance. These cells become heavily lignified and the outermost cells become suberized. The prickles remain on the plants throughout the entire season and even until the plant parts are completely weathered and decomposed (Fig. 1).

Development of the aerial stem

The histogens of the stem apex consist of the tunica and corpus (Figs. 28, 29). The tunica is a single layer of cells characterized by anticlinal cell divisions. This layer corresponds functionally to a dermatogen and gives rise to the epidermis. The second layer exhibits some anticlinal division, but this layer belongs more properly to the corpus, the massive central zone in which cell divisions are in random planes. The cells of the corpus are isodiametric, closely packed, without intercellular spaces and have thin walls, dense cytoplasm and large nuclei. These two zones are distinguishable as much as 120 microns back of the apex. Some meristematic activity is evident at this level.

Five procambium strands, arranged in a circle are distinguishable about 130 microns from the apex of the shoot (Fig. 30). Each procambium strand consists of thin walled, closely packed cells with dense cytoplasm and elongated, deeply stainable nuclei. The cells of the surrounding ground tissue are larger, more vacuolate, have relatively smaller nuclei and exhibit the beginnings of intercellular spaces. The cells of the cortex, external to the procambium ring, and of the central pith, are essentially similar. The cells of the epidermis are thin-walled and still meristematic at this level.

At a slightly lower level the strands increase in diameter by cell enlargement and cell division (Fig. 31). Increase in

cell size is especially apparent on the inner and outer side of the strand. The planes of cell division in the central region of a strand tend to be tangential, resulting in cambiform stratification.

Phloem and xylem elements are differentiated approximately simultaneously. Phloem elements are differentiated on both outer and inner sides of the procambial strand in the form of small, separate strands, each consisting of a few sieve tubes and companion cells. These phloem elements are differentiated early and can be distinguished from the thin walled procambial cells by the larger size and regular 4-6 sided shape of the sieve tubes, by the presence of sieve plates and by the associated small, 4-sided companion cells.

The protoxylem cells are located toward the inner side of the procambial strand, adjacent to the internal phloem groups. In cross section the protoxylem cells are 4-6 sided and have pronounced annular secondary wall thickening. The slender protoxylem trachea exceed the procambial cells in length. The annular secondary thickenings are at first very close together, but subsequent elongation of the cell greatly increases the interval between bands. Protoxylem consists primarily of annular and spiral vessels, whereas the metaxylem consists of pitted vessels. The very early initiation of cambiform cell division in the bundle obscures the limits of protoxylem and metaxylem (Fig. 32).

Interfascicular cambium develops by the reactivation of primary ray cells, beginning at the edges of the bundle and ultimately forming a complete bridge across the ray, connecting all bundles and forming a complete cambial cylinder. Primary phloem groups occur inside and outside the cambial ring. The outer phloem groups are small and closely arranged, the inner strands are more or less scattered. After complete differentiation of the interfascicular cambium, secondary phloem and xylem are laid down, increasing the circumference of the stem.

The mature stem is approximately circular in cross-sectional outline. The tissue systems will be described in centripetal order. The epidermis is a single layer of compact, closely fitting cells, regularly rectangular in outline and somewhat elongated radially (Fig. 33). The outer wall is slightly thickened and has a very thin layer of cuticle. Chlorophyll is present only in the guard cells. Anticlininal divisions in the young epidermis provide adjustment for increase in stem circumference. In the maturing stem, periclinal divisions of the epidermal cells occur in interrupted arcs, giving rise to a limited periderm immediately inside the epidermis. Repeated periderm formation by periclinal division of epidermal cells continues throughout the life of the plant, frequently repairing extensive damage caused by injuries.

Immediately adjacent to the epidermis or periderm, a single layer of chlorenchyma occurs, characterized by close

fitting, thin-walled cells, devoid of intercellular spaces on the outer side but having intercellular spaces on the interior side. These cells contain numerous chloroplasts (Fig. 33).

A band of collenchyma, 3-4 cells thick, occurs adjacent to the chlorenchyma. In longitudinal sections these cells are somewhat elongated. In both transverse and longitudinal aspects, the cell walls have pronounced thickenings at the corners (Fig. 33). The remainder of the cortex consists of 3-4 layers of large, thin-walled, parenchymatous cells with uniformly thin walls and large intercellular spaces (Fig. 33). Interspersed among the cortical parenchyma cells are isolated sclereids, of the same size as parenchymatous cells, but having thickened secondary walls and abundant pits.

The cortex is limited on the inside by a single layer of endodermal cells, slightly smaller and more regular in size as compared to the adjacent cortical parenchyma (Fig. 34). The endodermal cells have no intercellular spaces toward the outside of the stem and very small intercellular spaces on the inside. In longitudinal section the endodermal cells are elongated and contain elongated nuclei, numerous plastids and starch grains. Free-hand sections stained in iodine verify the presence of starch in the endodermis.

Immediately adjacent to the endodermis, in a position corresponding to pericycle, prominent fiber cells occur, singly and in interrupted groups (Fig. 14). They are the

last primary permanent tissues to differentiate in the stem. In cross section the fibers are 4-6 sided and have thick, lignified walls. The fibers are surrounded by parenchymatous cells which extend inward to the outer phloem groups. These undifferentiated cells may be designated as pericyclic parenchyma.

The phloem consists of sieve tubes, companion cells and some parenchyma. The sieve tubes arise from phloem initials by longitudinal divisions, which divide each phloem initial into two unequal cells; the larger becomes the greatly enlarged sieve tube, the smaller becomes the companion cell. The sieve tubes are 5-6 sided and have finely pitted sieve plates. The sieve tubes are greatly elongated, sometimes attaining a length 5-7 times their diameter. The companion cells are not as long as the sieve tubes, as the result of transverse septation. The phloem parenchyma consists of polygonal thin-walled cells (Fig. 34).

The cells of the interfascicular cambium are rectangular in cross section and somewhat elongated in longitudinal view. Derivatives of these cells differentiate into secondary xylem, phloem, and vascular ray parenchyma. The secondary xylem consists mostly of large, pitted vessels, the segments of which are two or three times their diameter. The tracheids are elongated, closely fitted cells with pointed ends and reduced pits. The tracheids and vessels comprise by far the greatest portion of the secondary xylem. Xylem parenchyma is also laid down in radial rows between radial rows of vessels and tracheids (Fig. 34).

The inner phloem strands, of primary origin, are scattered in an interrupted ring, adjacent to the primary xylem. These strands have been previously described. A zone of unspecialized parenchymatous cells, differing from the larger pith cells, occurs between and around the inner phloem. This zone which limits the pith on the outside and secondary xylem on the inside may be referred to as the perimedullary zone. Prominent lignified fibers, similar in every detail to the pericyclic fibers occur singly or in interrupted groups, adjacent to, or several cells remote from the inner phloem strands. The pith, which remains intact throughout the life of the stem, is composed of large, thin walled parenchymatous cells having abundant, large intercellular spaces (Fig. 34).

Development of the rhizome

Underground stems or rhizomes arise adventitiously from either vertical or horizontal roots by meristematic activity in the secondary phloem of the root. Cell division in this reactivated area is at first periclinal and anticlinal but later divisions take place in random planes. Continued meristematic activity produces a dome shaped meristem, the apical growing point. The thin walled, small, compact, actively growing cells are distinct from the adjacent, large parenchyma cells. The young shoot eventually emerges to the surface of the root.

The histogens of the stem apex of this adventitious "bud"

are very simple and consist of the tunica and corpus. The tunica is a single layer of narrow cells, characterized by anticlinal cell divisions. This layer corresponds functionally to a dermatogen and gives rise to the epidermis. The second zone, the corpus, exhibits some anticlinal cell division but consists essentially of isodiametric cells in which the cell divisions are in random planes. The corpus comprises the central or major portion of the meristem.

Lateral leaves of the underground stem have their origin near the apex of the promeristem. Leaf primordia appear as lateral emergences which elongate by marginal meristematic activity and fold over the active growing point. Usually one or two leaf primordia are microscopically visible on the adventitious bud before it emerges from the root. The differentiation of tissue systems follows the pattern of development previously described for the aerial stem.

The mature underground stem is histologically similar to the aerial stem. There are no spines or epidermal hairs. The epidermis is a single layer of closely fitting, somewhat elongated rectangular cells which lack chlorophyll. Periclinal division in interrupted arcs gives rise to a periderm immediately adjacent to the epidermis. Sloughing of the outer cells is accompanied by continued meristematic activity of the periderm. Superficial mechanical injuries are repaired by the activity of the periderm. If deeper seated injuries occur, reactivation of the cortical

cells produces wound callus.

The cortical parenchyma adjoining the periderm is approximately 8-10 cell layers in thickness and consists of large thin walled cells, large intercellular spaces, and scattered, isolated sclereids. The sclereids have thick secondary walls, and are about the same size as the surrounding parenchyma cells. All parenchyma cells contain abundant starch.

The cortex is limited internally by an endodermis. These cells are uniform in size, slightly smaller than the adjacent cortical parenchyma cells and have few and small intercellular spaces. Immediately adjacent to the endodermal cells, prominent sclerenchymatous cells occur, singly or in interrupted groups. These cells have thick, lignified walls, and are surrounded by small parenchymatous cells. Thus the pericycle consists of sclerenchyma and parenchyma.

The structure of phloem and xylem elements and of the cells of the pith is the same as in the aerial stem. The pith cells contain abundant starch.

Development of the root

The primary meristem of the radicle is an open type of promeristem. This zone of cells envelops the apex of the root in the form of a shallow cap. The outer or distal derivatives of meristematic activity enlarge and become a part of the root cap. The cells of the root cap are nearly isodiametric, slightly

elongated in the direction of growth, somewhat vacuolate, contain starch grains, and lack intercellular spaces. The conical root cap is several cell layers in thickness at the apex and decreases in thickness at the lateral sides (Fig. 16).

Derivatives of the promeristem differentiate into three histogens, dermatogen, periblem, and plerome (Fig. 15). In the region of initiation the outermost histogen, the dermatogen, consists of a single layer of very compact, closely fitting, isodiametric cells which undergo repeated anticlinal division, become elongated and eventually become the epidermis. The epidermal cells are closely fitting, devoid of intercellular spaces, and give rise to root hairs. The periblem is a zone immediately inside the dermatogen. In the region of initiation, the cells of the periblem are compact, closely fitting, and isodiametric, very similar to the cells of the dermatogen. The periblem arises as a result of divisions in the promeristem. At the time of initiation the periblem is only one or two cells in thickness and becomes a region of several layers by repeated anticlinal and periclinal divisions. These cells become greatly elongated, thin walled and vacuolate, and give rise to the cortex.

The plerome or innermost histogen of the root is derived from the central portion of the promeristem. The cells of the plerome undergo some longitudinal cell division and become considerably elongated. The plerome may be regarded as

procambium because most of the zone becomes differentiated into primary vascular tissues.

Some differentiation occurs in the plerome very near the apical initials. The vascular arrangement in the stele is triarch (Fig. 15). Annular protoxylem trachea occur adjacent to the uniseriate pericycle. Differentiation of xylem elements is centripetal. A few spiral elements and scalariform vessels are produced. Centripetal differentiation continues to the center of the stele and therefore, pith is absent.

The primary phloem occurs as strands radially arranged, between or alternating with the protoxylem arcs. These groups of primary phloem are separated from the xylem strands by parenchymatous tissue consisting largely of isodiametric cells. Frequently the distinction between phloem groups and surrounding parenchymatous cells is not well defined in the young root. The sieve tube elements are the first to differentiate adjacent to the pericycle. Companion cells are less clearly distinguishable at this stage than in the later-formed phloem. Sieve tubes and companion cells continue to be developed centripetally. The mature primary phloem of roots consists of sieve tubes, companion cells, and phloem parenchyma, all structurally similar to corresponding cells in stems. Primary phloem elements are smaller than secondary phloem elements.

The interfascicular cambium is progressively differentiated from the parenchymatous tissue lying between the primary xylem

and primary phloem groups, until a complete cambial cylinder is formed. The cambial layer is similar to that described in stems and consists of rectangular, closely fitting, densely cytoplasmic cells. Cambial activity produces secondary phloem and secondary xylem.

The periderm arises endogenously in the pericycle early in the ontogeny of the root and forms a complete layer. The primary endodermal and cortical cells are eventually sloughed off and the secondary cortex consists of secondary phloem and phelloderm.

The structure of the mature root is well illustrated by two-year-old vertical roots (Figs. 35, 36). The outermost three or four layers of cells, derived from the periderm are in the process of being sloughed off and exhibit all stages of disintegration. These cells are isodiametric in transverse section but somewhat elongated vertically and are entirely devoid of starch. The periderm is two to three cells in thickness and is devoid of intercellular spaces. These cells contain dense protoplasm and numerous starch grains.

Immediately inside the periderm is the many-layered secondary cortex, consisting of secondary phloem and phelloderm. The parenchymatous cells of the cortex vary greatly in size. They are largest on the side adjacent to the periderm and progressively smaller toward the inside. Large intercellular spaces are present. The cortical cells are filled with starch. The great starch storing capacity of this region is probably

responsible for the efficient shoot regeneration of this plant.

The cambial zone consists of 2-3 layers of rectangular, tangentially and vertically elongated cells, and contains the cambium and its most recent derivatives. The outer derivatives differentiate into secondary phloem, the inner derivatives into secondary xylem. The xylem consists of thick walled pitted vessels possessing oblique end walls, thick walled pitted tracheids with pointed ends, and thin walled parenchyma which contains starch. The tracheids comprise much of the center of the stele, which lacks a pith. The demarcation between annual rings is not as distinct as in perennial woody stems.

Horizontal or lateral roots arise endogenously in the pericycle, and their initiation, development, and mature structure corresponds in all respects to the vertical roots described above. Horizontal roots are not produced in such abundance as are vertical roots. The pericycle cells in the zone of root initiation first increase in radial diameter and divide tangentially. Subsequent cell divisions occur in random planes resulting in the formation of a root primordium, which elongates by the repeated division of an apical zone of cells. As the root primordium elongates, the cells of endodermis, cortex, and epidermis of the parent root are stretched and eventually ruptured by the emerging lateral

root which emerges practically at right angles to the parent root. Tissue differentiation in lateral roots follows the same pattern as in the parent root. The origin of roots from rhizomes follows closely the method of origin of lateral roots on other roots.

Development of Reproductive Organs

Floral ontogeny

Plants grown from seed initiate floral primordia in July and August, approximately in the middle of the growing season. On plants arising from perennial roots, no microscopic evidence of floral formation was found in one week old vegetative shoots. By the end of the second week, however, plants were found to have floral primordia.

The initiation of the organs of an individual flower is preceded by a slight broadening and flattening of the apex of the primordium. (Fig. 37). Meristematic activity on the periphery gives rise to calyx primordia, which elongate and curve inward until their apices touch (Figs. 38, 41). Rapid lateral growth of the enclosed disc-like apex pushes the calyx lobe tips apart (Fig. 42). The corolla is initiated by a second circle of zones of meristematic activity, immediately centripetal to the calyx and alternating with the calyx lobes (Fig. 43). The rudimentary corolla curves inward and

arches over the axis (Figs. 44,45). The stamens arise as a circle of swellings centripetal to the corolla (Figs. 44,45). The stamen primordia are adnate to the corolla and alternate with the lobes (Fig. 45). The two carpels arise as meristematic protuberances adjacent to the stamens (Figs. 45,46,47). The compound pistil consists of the united carpels, a short, thick style and a broad flattened two-lobed stigma (Fig. 48). In transverse aspect the ovary has two locules and an axial placenta bearing many ovules (Figs. 49,50). One raceme may bear a gradation from floral primordia to macroscopically discernible berries.

Gametogenesis

The young stamens consist at first of undifferentiated tissue. In two-week old shoots the sporogenous tissue is distinguishable as a layer of cells with denser, deeply stainable protoplasm and somewhat enlarged nuclei. Each archesporium at first consists of a single layer of hypodermal cells. The anther wall cells undergo periclinal division forming a wall 4-6 cells in thickness (Figs. 51,52,53). The initial archesporial cells also divide producing a second layer. The archesporial cells are arranged in four arcs, each having between 25-50 sporogenous cells in transverse section. The archesporia are separated by connective tissue. At maturity, each of the four pollen cavities is in the form

of an arc with columnar connective tissue on the concave side (Fig. 56). The round filament consists of approximately eight rows of elongated cells. The central vein ends in the connective tissue of the anther.

By the third week after emergence of shoots from perennial roots, somatic division of archesporial cells terminates. The entire outside row of cells of the arc differentiates into a single layer of binucleate tapetal cells (Fig. 53). The tapetal layer and some of the inner connective tissue disintegrates at maturity (Figs. 54, 55).

The first and second meiotic divisions occur in quick succession. Acetocarmine smears of anthers and sections of root tip from imbedded material give a monoploid chromosome number of 12 and a diploid number of 24. The members of the microspore quartets separate and each microspore becomes a binucleate pollen grain, containing the generative and tube nucleus (Figs. 54, 55). Each pollen grain has three pores. The pollen grain wall consists of a membranous intine and a firm, closely adhering exine (Fig. 55). Abundant pollen is available at the end of the 4th week of aerial growth arising from perennial roots. Estimates from sections of known thickness indicate that a single flower may have well over 300,000 pollen grains.

Ovule primordia are evident at the end of the second week of shoot growth from perennial roots. The first sign of ovule

formation consists of increased meristematic activity in localized regions, imparting an undulating outline to the placenta (Figs. 57-62). The ovules first become slightly elongated and pointed, then become curved by more rapid anticlinal cell division on one side and eventually become anatropous. A sub-epidermal cell enlarges and becomes the megasporocyte (Fig. 63). Integument primordia arise from the base of the ovule (Figs. 64-71). Enlargement of the macrospore mother cell is accompanied by the continued growth of the integuments until only the small micropylar opening remains between the integuments (Figs. 64-71). The macrosporocyte continues to enlarge until it is 5-6 times as large as the original archesporial cell and contains dense, deeply stainable cytoplasm and a large nucleus with several nucleoli (Fig. 64). The sporocyte is completely surrounded by the single layered nucellus. The first meiotic division places the daughter nuclei at opposite ends of the cell, without the formation of a cell wall (Figs. 65, 66). The second division occurs in the same axis producing four nuclei in a row, and transverse cell walls are formed between the four linear macrospores of approximately equal size (Figs. 67, 68). The three micropylar macrospores disintegrate and the functional macrospore at the antipodal end of the series gives rise to the embryo sac (Figs. 69, 70). This macrospore enlarges and its nucleus divides near the micropyle. One nucleus migrates to the distal end of the

sac and two more nuclear divisions occur. The mature embryo sac contains the egg, two synergids, the two polar nuclei and three antipodal nuclei (Fig. 71).

Pollination

The horse nettle plant has no specific flowering period. The plant produces flowers abundantly and continuously in the vicinity of Ames from the first part of June to the latter part of August. Some flowering continues until frost. The flowers usually close loosely during rainy periods or during the night. During optimum flowering periods the corollas remain active for a period of about four days. Acetocarmine smears of anthers disclosed meiosis on September 1, September 20, and October 14, 1941. Floral and vegetative development continue to some extent until frost. The flowers shed viable pollen the same day as they open. Viable pollen is available from an individual flower for a period of about four days after opening. Pollen is available on a raceme for a period of about 15.2 days (Table 1).

Pollen germination was tested in tap water, distilled water, 10% sucrose, 10% invertase, 10% dextrose and filtered juice of macerated stigmas. Only the last two gave some indication of the swelling associated with germination, but no tube growth occurred. Dr. Roy Bair kindly furnished two solutions (15-3, 15-4) the complete formulas of which have not as yet

become available.* These solutions gave 90% germination and considerable tube growth in 24 hours. Using pollen from newly opened flowers, tube growth was evident within 5 minutes in Bair's media. As high as 60-90% germination and tube growth occurred in 40-45 minutes at 29°C. With relative humidity of 54% and 74% at 29°C the pollen tubes were very commonly 40 times greater than the pollen diameter.

During the expansion of the flower, the pistil elongates and pushes through the staminal cone. Cross pollination may be accomplished by various insects, or possibly by wind. Bumble bees are among the most common visitors of the plant.

An attempt was made to determine whether horse nettle flowers were self pollinated or cross pollinated. Flowers selected at random in a large patch were emasculated previous to opening. All flowers thus treated opened, but without exception fell off. Flowers similarly treated during the following season and some of them artificially shaded, also dropped off. Individual flowers bagged in cellophane and shaded artificially opened and bloomed as usual and set viable seed. Flowers similarly treated but not shaded produced fewer berries with viable seed. Unopened flowers which were emasculated, the anthers allowed to dry slightly, the flowers then selfed, bagged in cellophane sacs and shaded, set viable

*Bair, R. A. Influence of weather on yield and growth of maize. Unpublished thesis (Ph.D.), Library, Iowa State College. 1940.

seed. Unopened flowers which were emasculated and cross pollinated and bagged in cellophane also set viable seed. Table 4 summarizes the data obtained in the pollination studies, which showed that viable seed may be produced by either self or cross pollination. It is probable that both types may occur.

Table 4

Response of Horse Nettle Flowers to Emasculation,
Self, and Cross Pollination (50 Flowers in
each Test)

Year	Treatment	No. of berries with variable seed
1938	Emasculated, previous to opening, full sun	none (abscized)
1939	Emasculated, previous to opening, full sun	none (abscized)
1939	Emasculated, previous to opening, shaded	none (abscized)
1939	Individual single flowers bagged before opening (self pollinated) full sun	10
1939	Individual single flowers bagged before opening (self pollinated) shaded	16
1939	Emasculated but pollinated immed- iately (selfed), shaded	8
1939	Emasculated but pollinated immed- iately (cross pollinated), shaded	18

Seed and fruit

The zygote develops a wall and elongates until it is 2-3 times as long as wide, then divides transversely to form a two celled pro-embryo (Figs. 72,73). The apical cell is isodiametric, the basal cell is longer than wide (Fig. 73). A transverse division of each cell produces four cells in linear arrangement (Fig. 74). The suspensor is derived from the basal cell of the group (Fig. 77). The division of the apical, second, and third cells results in the formation of an enlarged sphere, which becomes the main body of the embryo (Figs. 75,76). Prior to the initiation of organs, it is possible to distinguish the histogens, the dermatogen, periblem, and plerome, which give rise respectively to the epidermis, cortex, and stele (Fig. 77). The apex of the proembryo becomes flattened (Fig. 77). Accelerated cell division on the flanks gives rise to two lobes, the cotyledon primordia. The apical meristem of the axis becomes distinguishable as a dome shaped mass of meristematic cells in the depression between the rapidly elongating cotyledons. The proximal region of the embryo consists of the radicle and its root cap (Fig. 78).

The primary endosperm nucleus divides in advance of the zygote. After a period of free nuclear division and before the first zygotic mitosis, rapid cell division in the endosperm in random planes completely fills the embryo sac and envelops the

embryo. The embryo and endosperm cells are filled with reserve food, the nature of which was not tested except to ascertain that the cells lack starch.

The mature fruit is a green, spherical, bicarpellate berry with a central placenta and two locules. The calyx is persistent. An abscission periderm is present at the base of the mature fruit. A localized periderm also develops at the base of the style. The abscission periderm of both regions is discernible macroscopically on the fruit. The epidermal cells of young fruits are at first largely isodiametric, but as growth continues, cell division is very largely in a periclinal plane. The outer walls and to some extent the radial walls are heavily cutinized and the entire berry is covered with a firm, thick, cuticle. Epidermal hairs, glands, and other emergencies are lacking. The epidermis is one cell in thickness.

The major portion of the fleshy ovary wall consists of large, closely packed, moderately thick walled cells, with sparse intercellular spaces. The cells are nucleate, highly vacuolate, with sparse cytoplasm and numerous plastids and starch grains. The fleshy wall of mature fruits is about 25-35 cells in thickness. This tissue is traversed by 8-10 vascular strands, arranged in a circle, occupying approximately a median position in the ovary wall tissue. The seeds are imbedded in a watery mass of homogeneous, thin walled

parenchymatous cells, which tightly fill the entire locular cavity at maturity. This tissue is of placental origin and appears early in the development of the fruit, when the young berry is about 1/8 inch in diameter.

Vegetative Growth Cycle of Horse Nettle

Seed germination studies

Horse nettle seeds were collected in the vicinity of Ames, Iowa. Two main methods of preparing these seeds for storage or germination were used. In method A, fresh berries were crushed under water and violently agitated in water, then run through a coarse screen to separate the seeds. The seeds were washed in several changes of water and either placed in the germinator immediately, or dried and stored. In method B, the old dried berries which were collected in the field, or berries which had been stored in the laboratory, were crushed and the seeds separated by means of sieves and an air blast.

Seeds were germinated between moist blotters, four germination readings were made at seven day intervals. The tests were concluded at four weeks unless otherwise stated. In order to determine the optimum temperature for germination, seeds were germinated at several temperatures. Mature berries were gathered October 15, 1937, the seeds removed from berries

according to method A, spread out on paper, allowed to dry at room temperature for two days, and stored in the laboratory at room temperature for three months. The summarized results of germination tests at five different temperatures, in three different substrata, and from three different collection areas are given in Table 5.

Horse nettle seeds were found to have a higher percentage of germination and produce stronger seedlings at 35° C. than at any other temperature tried. Therefore, subsequent germinations were made between moist blotters at a constant temperature of 35° C. unless otherwise indicated.

Some germination is evident soon after a test is begun but, extensive germination is not evident for several days as shown in the following experiment. Fresh seed was removed from the berry by method A, dried at room temperature in the laboratory for two days and stored in a manila envelope at room temperature in the laboratory for three months and then tested. Germination was 2% at the end of 48 hours, 20% at the end of 72 hours and 50% at the end of 96 hours.

Horse nettle seeds undergo some after-ripening in the berries. This is shown by the following tests. The berries were gathered in the field and after thorough mixing were equally divided at random. One lot was prepared for germination immediately, according to method A. The other lot was

Table 5

Effect of Temperature, Substrate, and Collection Areas Upon Horse Nettle
Seed Germination

Temperature	Substratum	Percentage of germination (4 lots of 100 seeds in each column)								
		Area A			Area B			Area C		
		Collected from	Collected from	Collected from	Collected from	Collected from	Collected from	Collected from	Collected from	Collected from
10° C. Constant	Blotter	0	0	0	0	0	0	0	0	0
10° C.	Sand	0	0	0	0	0	0	0	0	0
10° C.	Soil	0	0	0	0	0	0	0	0	0
20° C.	Blotter	.25	0	.5	3.0	2.25	.75	1.0	0	0
20° C.	Sand	3.25	.25	1.75	7.25	7.75	6.75	4.25	1.0	.25
20° C.	Soil	1.25	1.75	2.75	8.75	6.5	7.75	2.5	3.0	.75
30° C.	Blotter	64.5	61.0	62.75	74.25	61.5	68.25	77.5	65.25	60.75
30° C.	Sand	65.25	59.0	60.75	95.75	72.75	65.75	79.5	73.5	69.5
30° C.	Soil	60.0	66.75	62.75	73.5	61.75	62.25	56.75	54.25	59.0
25-35° C. Alternating	Blotter	70.0	67.75	65.25	55.25	58.25	61.75	61.0	54.0	54.75
25-35° C.	Sand	61.0	58.0	55.25	66.0	69.25	66.75	57.75	61.0	50.0
25-35° C.	Soil	52.75	59.75	54.75	60.25	63.0	60.5	54.25	65.25	52.0
35° C. Constant	Blotter	88.5	85.5	88.0	69.5	76.5	69.0	74.75	75.75	91.75
35° C.	Sand	85.25	82.25	87.25	84.25	91.75	84.0	91.0	92.25	94.75
35° C.	Soil	77.25	81.5	76.5	97.5	86.75	86.0	90.0	82.25	92.5

stored in the laboratory in an open container at room temperature for six months, after which they were crushed according to method B, and the germination tests were made. Summarized results of these tests are shown in Table 6.

Table 6
Effect of After-Ripening on Horse Nettle
Seeds

Date of Collection	10 lots of 100 seeds each germinated at 35°C.	
	% germination direct from field	% germination after 6 months laboratory storage
July 7, 1938	0	0
July 14, 1938	0	0
July 21, 1938	0	1.9
July 28, 1938	0	5.9
August 8, 1938	0	9.1
August 24, 1938	43.2	73.1

After-ripening was also shown in another experiment in which approximately 200 horse nettle plants were hoed off at the ground line on August 6, 1938 and the plants divided into two equal lots. The berries were picked from lot 1, the seeds removed according to method A, and germinated between moist blotters at 35° C. The berries in lot 2 were allowed to dry naturally in the field on the plants, picked after 6 weeks and the seeds removed according to method B. No germination was obtained from lot 1, whereas lot 2 gave 13.7% germination.

Mature horse nettle seeds exhibit no delayed dormancy.

Seeds from mature berries secured by method A were washed and tested immediately. The results are shown in Table 7.

Table 7
Germination of Horse Nettle Seeds Showing
Absence of Delayed Dormancy

Date of Collection and germination test	Percentage of Germination (10 lots of 100 seeds each at 35° C.)
August 15, 1938	19.5
August 20, 1938	27.5
August 27, 1938	30.375
September 3, 1938	30.75
September 10, 1938	28.75
September 17, 1938	39.875
September 25, 1938	57.5
October 1, 1938	83.75

A study was made to determine how early in the season viable seed is produced under field conditions. Berries were collected, thoroughly mixed and divided into two equal lots. The seeds were obtained from lot 1 by Method A, and tested immediately. Lot 2 was stored in the laboratory in an open container, at room temperature for six months. The seeds were removed according to method B and germinated. Results are given in Table 8.

Table 8
Production of Viable Horse Nettle Seed
1938-1940

Date of Collection		10 lots of 100 seeds each germinated at 35° C.	
		Percentage germination direct from field	Percentage germination after 6 mo. laboratory storage
July 14	1938	0	0
	1939	0	0
	1940	0	0
July 21	1938	0	.7
	1939	0	1.1
	1940	0	.3
July 28	1938	0	.9
	1939	0	1.4
	1940	0	2.4
August 4	1938	0	3.2
	1939	0	1.1
	1940	0	1.6
August 11	1938	.6	1.1
	1939	.5	1.7
	1940	1.1	4.4
August 18	1938	1.7	1.9
	1939	2.7	7.7
	1940	4.2	10.1
August 25	1938	8.3	28.0
	1939	4.4	17.9
	1940	6.1	31.1

Horse nettle seeds show a wide tolerance to different depths of planting. Berries were gathered March 29, 1940, the seed removed according to method A and dried for 24 hours at

room temperature in the laboratory. The seeds were planted in moist sand at various depths and germinated at 35° C. The results are shown in Table 9.

Table 9
Effect of Various Depths of Planting on Emergence
of Horse Nettle Seedlings

Depth of planting	Percentage germination per 1000 seeds at 35° C. (10 lots of 100 seeds each)
Blotters (check)	41.7
1/8 inch	41.0
1/4 inch	40.0
1/2 inch	47.0
3/4 inch	43.0
1 inch	45.0
1 1/4 inches	46.0
1 1/2 inches	11.0
1 3/4 inches	21.0
2 inches	16.0
2 1/2 inches	10.0
3 inches	5.0
3 1/2 inches	2.0
4 inches	0
4 1/2 inches	0
5 inches	0
5 1/2 inches	0

Some evidence on the longevity of horse nettle seed under laboratory storage conditions was obtained by an experiment conducted from 1936 to 1944. Mature horse nettle berries were gathered on October 7, 1936 and the seeds removed by method A. The seeds were spread on large blotters and allowed to dry at room temperature in the laboratory for 24 hours. They were then stored in a manila envelope in the dark, on the laboratory shelf until tested. The results are shown in Table 10.

Table 10

Longevity of Horse Nettle Seed Under Laboratory
Storage Condition. Seed gathered October 7,
1936.

Date of Germination	Percentage of germination at 35° C. (10 lots of 100 seeds each)
October 25, 1936	93.7
March 9, 1937	85.0
February 8, 1938	81.7
February 2, 1939	80.5
January 12, 1940	79.0
January 28, 1941	60.0
January 14, 1942	28.2
January 16, 1943	17.2
January 19, 1944	2.0

Another lot of seed which was collected in November, 1936, removed from the berry according to method A, dried at room temperature in the laboratory for 24 hours, stored in a manila envelope on the laboratory shelf in the dark at room temperature until the test was made in 1943. Germination results on this stored seed are shown in Table 11.

Table 11
Decline of Germinating Ability of Stored
Horse Nettle Seed

Date of Collection	Percentage of Germina-	Percentage of Germina-
	tion in 1936 (10 lots of 100 seeds each at 35° C.)	tion in 1943
November 3, 1936	94.0	3.6
November 18, 1936	73.8	2.1
November 21, 1936	83.1	1.2
November 28, 1936	89.7	1.9

To supplement these longevity data a few horse nettle berries were removed from dated herbarium specimens in 1943, the seeds removed immediately according to method B and tested for germination. Origin of samples, date of collection, and resultant germination are given in Table 12.

Table 12
Longevity of Horse Nettle Seeds in Stored
Herbarium Specimens

Town and County	Date of Collection	Germination (35°C.)
Wheatland, Clinton	Sept. 1895	0
_____, Decatur	Sept. 1895	0
Ames, Story	Sept. 1898	0
Afton, Union	Sept. 1902	0
Harlan, Shelby	Oct. 1913	0
Storm Lake, Buena Vista	Sept. 1918	0
Oxford, Johnson	Aug. 1920	0
_____, Sac	April 1922	0
LeMars, Plymouth	Oct. 1923	0
_____, Sac	Oct. 1924	0
Indianola, Warren	Sept. 1929	0
Laurens, Pocahontas	Aug. 1921	3.67 (4 out of 109)
_____, Wright	Oct. 1930	20.45 (9 out of 44)
Ames, Story	Oct. 1936 (author)	4.5 (18 out of 400)
Ames, Story	Nov. 1937 (author)	7.0 (28 out of 400)
Ames, Story	Sept. 1938 (author)	13.0 (52 out of 400)

Germination is usually lower in lots of "lighter" seed than in lots of heavier, larger seed. This was ascertained by the following tests. Seeds were removed from berries by method A, dried in the laboratory at room temperature for 24 hours and stored in a manila envelope in the laboratory for 3 months. The "check" seed was a random sample from the storage packet. The "hand picked" seed was selected according to large size and plumpness of the seed. The "blown" seed was prepared by using a calibrated machine in the seed laboratory. The results of germination tests are shown in Table 13.

Table 13

Effect of Cleaning by an Air Blast Upon
Germinating Ability of Horse Nettle
Seeds

Method of Seed Preparation	Percentage germination (10 lots of 100 seeds each at 35° C.)
Check (no seed selection)	42.2
Hand picked	47.2
Blown, 5 minutes at 20	49.0
Blown, 5 minutes at 30	50.2
Blown, 5 minutes at 40	59.2
Blown, 5 minutes at 50	73.2

If the horse nettle berry is well matured as judged by its yellow color, the size of the berry is correlated with the germination of the seeds. Berries gathered October 3, 1936 were measured and the seeds removed by method A. The seeds were dried at room temperature for 24 hours, and germination tests made at 35° C. The results are shown in Table 14.

Table 14
Effect of Berry Size on Seed Germination

Berry diameter in centimeters	Percentage germination (8 lots of 100 seeds each at 35° C.)
1/2 - 1	87.1
1/2 - 1	85.5
1 - 1 1/2	88.0
1 - 1 1/2	89.75
1 1/2 - 2	94.0
1 1/2 - 2	93.37

Water comprises the greatest portion of the juicy horse nettle berry. Fresh berries were collected October 6, 1937, measured, weighed and allowed to dry at room temperature in the laboratory. They were then crushed, the seeds removed according to method B and weighed. Germination tests were also made. The results obtained are shown in Table 15.

Table 15

Effect of Berry Size on Water Content,
Seed Weight and Germination

Sample No.	Berry Diameter in Centimeters	Green Wt. of 50 Berries	Percent of water per 50 berries	Air dry weight of seed from 50 berries	Percentage of germination per 400 seeds at 35°C. (4 lots of 100 seeds each)
1	1 - 1 1/2	71.0 gm.	84.6	4.3 gm.	86.5
2	1 - 1 1/2	71.8 gm.	81.6	4.5 "	80.25
3	1 1/2 - 2	108.4 "	83.2	8.5 "	79.25
4	1 1/2 - 2	110.7 "	82.3	8.7 "	84.75

Horse nettle seeds germinate very slowly or not at all at a temperature unfavorable for growth, but upon transfer to a more favorable temperature they immediately resume rapid growth. The berries for an experiment were collected in November, 1940, and the seeds removed from the berries according to method A, allowed to dry in the laboratory for one week at room temperature. Triplicate samples of the seeds were then placed (1) between moist blotters, (2) in sterilized sand, (3) in sterilized soil, and placed at 10°, 20°, and 30° C. germinating temperatures. After one month, the samples were moved to a 35° C. germinator. The results are shown in Table 16.

Table 16

Effect of Transferring Germinating Horse Nettle
Seeds from a Lower to a Higher Germinating
Temperature

Sample Number	Substrate & duration of test	Germination Temperature (Constant)	Percent of germination per 1000 seeds (10 lots of 100 seeds each)	Trans.: for 1 month to 35° C.	Add. per 1000 seeds	Total germ. percent per 1000 seeds
1	Blotter, 1 mo.	10°C.	0	"	660	66.0
2	Sand, 1 mo.	10°C.	0	"	631	63.1
3	Soil, 1 mo.	10°C.	0	"	638	63.8
4	Blotter, 1 mo.	20°C.	.30	"	770	77.3
5	Sand, 1 mo.	20°C.	3.0	"	772	80.2
6	Soil, 1 mo.	20°C.	1.1	"	580	59.1
7	Blotter, 1 mo.	30°C.	64.5	"	45	69.0
8	Sand, 1 mo.	30°C.	65.2	"	10	66.2
9	Soil, 1 mo.	30°C.	60.0	"	8	60.8

Seed viability varies among different patches of horse nettle plants. Berries were collected from five separate areas on October 16, 1937 and the seeds removed from the berries by method A. The seeds were dried at room temperature in the laboratory for 48 hours, and germination tests were made at 35°C. The variations in germination are shown in Table 17.

Table 17

Variability in Germination of Horse Nettle Seeds
Collected in Different Areas

Place of Collection	Percentage germination per 1000 seeds 10 lots of 100 seeds each (35°C.)
Ash Avenue	93.8
Sawtell Farm	79.5
Stafford Farm	83.1
College Pasture	49.2
North College Pasture	94.7

The effect of several well known preparations used for seed treatment was tested. Berries were collected on October 12, 1941 and the seeds removed by using method A. The seeds were dried at room temperature in the laboratory for 24 hours and were stored in a manila envelope until January, 1943, when the tests were made. The seeds were treated with the dust, shaken for 5 minutes, the excess dust screened off, and germination tests made. Zinc oxide gave consistent increases in germination over an untreated check. The results are shown in Table 18.

Table 18
Effect of Seed Treatments on Horse Nettle
Seeds

Seed treatment material	Germination per 1000 seeds (35°C.) (10 lots of 100 seeds each)
Check (no treatment)	30.2
Spargon	18.1
Semesan Jr.	15.0
New Improved Ceresan	0
Red Copper Oxide	21.7
Zinc Oxide	39.3

Germination of horse nettle seeds is usually lower in the spring than the preceding fall. Berries picked October 8, 1937 and kept outside for six months under various conditions, showed a wide variation in germination. The results of different lengths of outdoor storage conditions are shown in Table 19.

Table 19

Effect of Various Outdoor Storage Conditions Upon Germination of Horse Nettle Seed

Sample No.	Treatment	Percent of germination at 35°C. (10 lots of 100 seeds each)
1	Germination direct from berry (date)	73.0
2	Removed from berry, dried room temp., 2 days	50.5
3	" " " " " " " " 1 week	45.7
4	Seeds in berries, top of ground, 1 month Nov.	51.0
5	" " " " " " " " 2 months Dec.	26.0
6	" " " " " " " " 3 months Jan.	45.5
7	" " " " " " " " 4 months Feb.	50.2
8	" " " " " " " " 5 months (March)	38.5
9	" " " " " " " " 6 months (April)	38.7
10	Seeds buried in berries, 1 month (Nov.)	91.5
11	" " " " " " " " 2 months (Dec.)	71.0
12	" " " " " " " " 3 months (Jan.)	72.5
13	" " " " " " " " 4 months (Feb.)	72.5
14	" " " " " " " " 5 months (March)	56.0
15	" " " " " " " " 6 months (April)	45.0
16	Seeds removed from berries, buried 1 month (Nov.)	42.7
17	" " " " " " " " 2 months (Dec.)	39.5
18	" " " " " " " " 3 months (Jan.)	41.7
19	" " " " " " " " 4 months (Feb.)	40.5
20	" " " " " " " " 5 months (March)	39.7
21	" " " " " " " " 6 months (April)	38.6
22	Seeds removed from berries, top of ground, 1 month (Nov.)	56.7
23	" " " " " " " " 2 months (Dec.)	35.5
25	" " " " " " " " 3 months (Jan.)	41.5
26	" " " " " " " " 4 months (Feb.)	35.5
27	" " " " " " " " 5 months (March)	49.5
	" " " " " " " " 6 months (April)	46.7

Establishment of the seedling

Seedlings do not appear in the field until fairly high temperatures prevail. Seedlings were commonly observed during field studies in June. Under controlled laboratory conditions at 35° C. on moist blotters, seed which had been stored under laboratory conditions for one month exhibited noticeable swelling after 24 hours. The first macroscopic sign of root growth appeared after two days in the germinator. After three days germination had reached about 3% and after four days about 16%. This is increased to about 50% at the end of the fifth day. A very dense zone of root hairs becomes macroscopically evident about 2-3 mm. from the root tip. The root hair reaches maximum expansion about 1 centimeter from the root tip. After reaching maximum root hair growth, the activity of the root hairs is curtailed and lateral roots arise. Germination is rapid under favorable conditions and by the end of one week the slender seedling is about $\frac{1}{4}$ - $\frac{1}{2}$ inch long. Variations in time of collection, in maturity of the seed, in storage conditions preceding germination, and in temperature and nature of the substratum, all influence germination.

The average water intake of air-dry seed during germination, and the subsequent loss in weight during germination are shown in Table 20.

Table 20

Water Intake and Loss in Weight of Germinating
Seeds (10 lots of 100 Seeds per Lot)

Av. wt. of 100 air dry seeds (grams)	Av. wt. of 100 seeds after soak- ing 24 hrs. (gms.)	% inc.	Loss in weight in grams		
			48 hrs.	after 72 hrs.	1 wk.
1.076	2.022	87.9	1.968	1.952	1.832

This loss in weight may be presumed to be due to respiration.

Seed which had been stored under laboratory conditions for one month was planted in blotters, sterile sand, and sterile soil and placed in a germinator at 35° C. The seedlings began to emerge from sand and soil in from 5 - 7 days. The hypocotyledonary arch of the seedlings emerges and the cotyledons are usually freed from the seed coat as the arch pushes up through the substratum. However, the seed coat often persists on the cotyledons until mechanical rupturing takes place. Upon liberation from the seed coat the slender linear - lanceolate cotyledons serve as the first photosynthetic leaves. The average length of one month old seedlings of horse nettle, grown in blotters, in sterile sand and in sterile soil is shown in Table 21.

Table 21

Average Length of One Month Old Seedlings
of Horse Nettle (100 Measurements)

Germination medium	Length of Seedling (Cm.)
Blotter	6.4
Soil	6.2 (removed from soil)
Sand	6.7 (removed from sand)

Seeds which had been stored under laboratory conditions for one month and gave a germination of 93.1% were planted in blotters, sterile sand and sterile soil and germinated at 35°C. The results are shown in Table 22.

Table 22

Relation Between Germination in Blotters and
Appearance of Seedlings in Sterile Soil
and Sterile Sand (10 lots of 100
seeds each)

Days at 35° C.	Germination percentage			Remarks
	Blotter	Sterile Sand	Sterile Soil	
1	0	0	0	General swelling of seed
2	10	0	0	Root emergence in some seeds
3	30	0	0	Noticeable germination in blotters
4	162	0	0	Rapid growth in blotters
5	480	38	2	Seed coats usually removed in sand as hypocotyl pushes up
6	673	216	129	
7	875	543	318	Some secondary roots on seedlings
28	923	889	864	

The above table shows that germination in blotters precedes by several days the appearance of seedlings in either sand or soil.

Horse nettle seedlings in the greenhouse and the field are subject to "damping off" diseases. Preliminary study indicates that the mortality in the field may be extremely high and may account to some extent for the slow spread of this weed under our conditions. Table 23 shows the mortality of seedlings in sterilized and non-sterilized field and greenhouse soil. A germination test showed an average germination of 92% (4 lots of 100 seeds each). The greenhouse studies were made by using

garden soil, sterilized with steam, chloropicrin, and carbon bisulphide. The two liquids were applied at the rate of 2 cc. per four inch pot of soil. After treatment the pots were covered with waxed paper for two days, then aerated and planted. The field soil was treated by injecting the liquids into holes six inches deep, spaced 15 inches apart. The holes were tamped shut with the heel and covered for one week with tar paper. The tar paper was removed one week before planting. The results are shown in Table 23.

Table 23
Susceptibility of Horse Nettle Seedlings to
"Damping Off" Organisms. (10 lots, 100
seeds each)

		Total No. of Plants per 1000 seeds	% Germ.
Greenhouse			
Garden soil, not treated (check)		273	27.3
" " sterilized (steam)		861	86.1
" " " (chloropicrin)		773	77.3
" " " (carbon bisulphide)		691	69.1
Field			
Field soil not treated (check)		130	13.0
" " treated (chloropicrin)		708	70.8
" " " (carbon bisulphide)		669	66.9

Perennial growth habits of horse nettle

In Iowa, horse nettle occurs naturally only as an herbaceous perennial which freezes back at least to the ground line. If plants are taken up and placed in the greenhouse in the fall, they continue vegetative activity throughout the winter. Horse nettle appears year after year in the same area by growth from adventitious shoots from the perennial root system. Reference is frequently made in the literature that horse nettle plants always appear late in the spring, seldom appearing until all danger of frost is over. This apparently refers to shoots from old established roots as well as to seedlings. Table 24 gives the result of six years observation on the date of appearance of horse nettle in a field at Ames, Iowa.

Earliest horse nettle sprouts observed during this study were found March 19, 1941 in a sheltered location at Ames. A few very small seedlings were also found at that time. Late frosts killed both shoots from established roots and seedlings that year.

Appearance of horse nettle in the spring is dependent upon location, soil type, exposure and soil temperature. In 1938 horse nettle first appeared in the experimental area at Ames on June 2nd; it appeared on May 16th near the college greenhouses, in a sandier, more protected and warmer site. In 1942, horse nettle had appeared in the experimental area on April 26

Table 24

Chronology of Horse Nettle 1936 - 1942 Inclusive (College Pasture)

	: 1936	: 1937	: 1938	: 1939	: 1940	: 1941	: 1942
First appearance of new shoots from old roots	: June 25	: June 14	: June 2	: May 1	: May 10	: May 9	: April 26
First macroscopic flower buds	: June 7	: June 28	: June 11	: May 18	: May 23	: May 24	: May 9
First flowers open	: June 15	: July 12	: June 18	: June 1	: June 6	: June 8	: May 19
First blossoms drop	: June 20	: July 16	: June 23	: June 4	: June 11	: June 11	: May 24
First Fruits 2/16 in. in diameter	: June 25	: July 24	: July 1	: June 23	: June 20	: June 26	: June 14
First Fruits $\frac{1}{4}$ - $\frac{1}{2}$ in. in diameter	: July 20	: Aug. 12	: July 30	: July 19	: July 7	: July 9	: July 17
First successful seed germination	: Aug. 13	: Aug. 23	: Aug. 12	: Aug. 15	: Aug. 11	: Aug. 19	: Aug. 14
Fruits start to turn yellow	: Aug. 18	: Aug. 26	: Aug. 20	: Aug. 19	: Aug. 20	: Aug. 22	: Aug. 26

but the plants did not appear until May 26 in a level fall-plowed field at Ames. In 1936, when the first flowers opened in the experimental area on June 15, plants were in full bloom at Clarinda and Leon, Iowa. In 1938 plants were coming up in level fields in East Pottawattamie County on May 17, but at Ames they did not appear until June 2. In 1938, plants were blossoming on May 15th in Clarke County near Osceola, and on June 18th at Ames. Thus, many factors influence the dates of spring appearance and blossoming time of horse nettle. The plants appear earlier on lighter soils, in protected areas or on southern slopes than on heavier soils, on open areas and on northern exposures. They appear earlier in the southern part of the state than in central or northern Iowa. They appear earlier in open fields, than in fields heavily shaded with crops.

The suggestion has been made that the vertical roots freeze back every year to a depth of 12-18 inches and that it is from below this depth that the next season's shoots arise. The additional growth required was supposed to be at least one of the reasons for the late appearance in the season. This freezing back, which may be a factor in some years, has not been found to occur in the six years that the plant has been under observation here. Figures 5 and 8 show vertical roots producing young shoots practically at the ground line where the stem

of the previous year can still be seen. This has been consistently observed throughout every season that the plant has been under study.

Even though freezing was not found to inhibit shoot production from old established roots in the uppermost soil layers, the roots are nevertheless susceptible to freezing injury, as shown in Table 25. Roots were gathered on the designated dates, cut into one inch pieces, subjected for 24 hours to the indicated temperature and potted in greenhouse soil. Readings were made at the end of one month, during which time the greenhouse temperature was kept as nearly as possible at 60-70 degrees F.

Table 25
Influence of Temperature on Production of Shoots

Date of Collection	Number of shoots produced per 50 root pieces					
	Temperature (24 hrs. duration)					
	70° F.	45° F.	33° F.	+20° F.	-20° F.	
March 1	21	34	27	-	-	
April 15	31	27	39	-	-	
June 1	37	39	43	-	-	
August 1	40	36	37	-	-	
September 1	39	44	29	-	-	
October 26	27	36	36	-	-	
December 1	32	38	29	-	-	

The table shows that injury to rootstocks may occur, especially by quick freezing and thawing. Roots exposed by fall plowing have repeatedly and consistently been found to be killed by the ensuing winter. However, when roots are undisturbed and protected by soil, very little injury results.

Experiments conducted during three successive growing seasons indicate that horse nettle roots undergo no extended dormant periods. The collections of roots were cut into 2 inch pieces, potted in 8" pots of greenhouse soil and kept for one month at greenhouse temperature of 60-70° F. Results are shown in Table 26.

Table 26

Relation of Date of Collection of Roots to
Emergence of Shoots in the Greenhouse

Time of Collection	Days Required to Produce Shoots		
	1938	1939	1940
January	12	11	11
February	10	14	12
March	12	12	14
April	11	13	12
May	13	12	10
June	9	11	14
July	14	12	11
August	10	14	13
September	13	11	12
October	11	11	12
November	13	12	9
December	11	12	12

These experiments were further supported by field observations during the growing season. Repeated mowing or cultivation during the active growing season is invariably followed by the production of shoots from perennial roots. Thus climatic conditions, especially temperature, are probably responsible for the periodic activity of the plant under

natural conditions. Lack of a dormant period in the roots is closely matched by lack of a dormant period in the seed as is shown in Table 7.

Horse nettle plants are seldom seen early in the spring. If seedlings or shoots do appear early in the spring, and a late frost occurs, both seedlings and shoots from perennial roots are easily killed. Vegetative activity is continued until killing frost, as is evidenced by formation of new shoots from roots which have had previous shoots removed by cultivation. Mature seeds in berries on the plant are not appreciably injured by frost.

An experiment was conducted for two consecutive years to determine the effect of lengths of root pieces upon the ability to produce shoots. The roots were gathered March 1 (dormant period), June 1 (active growing period), September 15 (previous to killing frost) and December 1 (after killing frost). The roots were cut into $\frac{1}{2}$ inch, 1 inch and 2 inch pieces and potted in eight inch pots of greenhouse soil. Observations were made at the end of one month, during which time the greenhouse temperature was kept at 60-70° F. Fifty pieces of each length of roots was used in each test. Results are shown in Table 27.

Table 27

Number of Shoots Produced by Roots of Various Lengths, 1939-1940

Date of Collection	Length of Root Pieces	Shoots from 50 Pieces of Roots	
		1939	1940
March 1	$\frac{1}{2}$ "	20) First shoots	16) First shoots
	1"	42) in 13 days	38) in 11 days
	2"	46)	43)
June 1	$\frac{1}{2}$ "	14) First shoots	18) First shoots
	1"	41) in 12 days	44) in 14 days
	2"	48)	47)
September 15	$\frac{1}{2}$ "	18) First shoots	13) First shoots
	1"	50) in 13 days	40) in 12 days
	2"	44)	42)
December 1	$\frac{1}{2}$ "	16) First shoots	19) First shoots
	1"	32) in 12 days	34) in 12 days
	2"	46)	33)

Samples taken at four different stages in the life of the plant showed no marked difference in their ability to produce shoots. Of the three lengths tested in Table 27 the two inch pieces produced the greatest number of shoots, as well as the largest, most vigorous shoots.

Major Fungous Diseases and Insects Found on Horse Nettle

The most prominent pathogen found during the years that the host has been under observation is Eriayphe cichoracearum D. C. This pathogen, which has a wide host range, was first reported as occurring on horse nettle by Anderson (45) who observed the conidial stage in 1905. Late in the season the fungus becomes very conspicuous, covering primarily leaves, but also stems, pedicels and calyx with such a heavy growth of mycelium and conidia, that severely infected plants assume a hoary appearance. Usually, even severely infected leaves retain their characteristic shape but malformed and distorted leaves are not uncommon. Extremely heavy infection may produce complete defoliation of the entire plant. Heavily infected leaves are shown in Figure 3. This disease, even though severe and consistently present, is not a limiting factor to the growth and reproduction of the host.

A much less severe disease which has been observed infrequently is caused by Puccinia tubulosa (Pat and Gaill) Arthur & Fromme. This fungus was first reported as occurring on horse nettle in Iowa by Layton (44) in 1932, and has been reported by Arthur (2) to be a widespread tropical rust, occurring not only upon tropical solanaceous plants, but upon a wide variety of hosts in other families.

During the season of 1939 several horse nettle fruits were observed to have a disease very suggestive of the blossom and rot of tomatoes. The first visible symptoms consisted of abnormal green, water spots on the fruit at the point of attachment of the style. These spots generally enlarged so that eventually one-third or one-half of the fruit became necrotic. The necrotic area later became brown and shrivelled in appearance. Numerous isolations made from such infected fruits yielded several organisms, the pathogenicity of which was not ascertained. The host involved is not cultivated or valuable, and the fruit and rot is not a limiting factor in the life of the plant, therefore, further investigation seemed unnecessary for the present study.

Another disease consistently observed in both fields and greenhouse plantings is a seedling "damping off" caused by an unidentified fungus.

Several species of insects have been consistently found on horse nettle in Iowa during the present study. By far the most common insect found was the cucumber or potato flea beetle, Epitrix cucumeris Harris. The adult insect punctures numerous very small holes in the leaves. Where insect numbers become great, considerable damage is done. Young succulent leaves are often severely damaged. Leaves damaged at least in part by this insect, are shown in Figure 9. This insect is of wide distribution and attacks other solanaceous hosts, as well as a wide

variety of other plants including melons, cucumbers, raspberry, turnips, cabbage and others. While this insect frequently causes considerable leaf damage to horse nettle plants every year, it does not appear to become a limiting factor in its growth and spread.

Another insect frequently observed on this plant is the common Colorado potato beetle, Leptinotarsa decemlineata Say. Eggs, larvae and adults have been found frequently on the plant. The young, reddish colored larvae are voracious feeders and cause the most damage to the leaves of the plant. Part of the leaf damage shown in Figure 9 is due to these insects. Young, succulent plants and new shoots are often completely defoliated. The damage to horse nettle, however, is not comparable to the damage the insect inflicts on potato. In no instance have they been observed to kill out established areas of horse nettle.

Various species of plant lice, aphid sp., are also consistently found on horse nettle. Genera include Aphis, Macrosiphum and Myzus among others. Only the agamic forms of the insects were observed. Those insects are found throughout the season in various stages of development, indicating that several generations occur during the season. The aphids were invariably attended by ants.

Two other insects found on the plant are two species of blister beetles, Epicauta pennsylvanica and Epicauta cinerea. Adult beetles of both species are known to defoliate potatoes,

but various other plants are also attacked.

The most interesting insect encountered upon horse nettle is a gall moth, Gnorimoschema lavernella Chambers. The moths make their appearance about the time the first horse nettle plants begin to bloom. They are usually found around the plants at dusk. They lay their eggs upon the surface of the ovary or young fruit. The larvae, upon hatching presumably eat their way into the young ovary. Sections of young ovaries have revealed the presence of larvae, presumably of this insect. The invaded berry continues to grow to practically normal size. The young larvae gradually eat out the entire interior of the berry. The larva becomes full grown, but before pupating it eats a small passageway to the surface of the berry. The hole is then closed with a fine sheet of opaque material. After pupation, the adult moth crawls through the passageway, pushes out the surface covering and escapes. In the vicinity of Ames the moths emerge during July and August. This moth has been observed every year throughout the course of this study, but usually not in very great numbers, becoming very numerous only in 1939. Its occurrence ('36-'42 inclusive) in the vicinity of Ames is shown in Table 28. Three random collections of 500 berries each was made every year in three areas near Ames (College pasture, Sawtell farm, Stafford farm).

Table 28

Number of Moth Pupae and Larvae Collected at
Three Separate Areas 1936-1942 inclusive.
500 Berries Per Area

Year	Area			Total number larva and moths per 1500 berries
	A.	B.	C.	
1936	7	5	6	18
1937	9	8	6	23
1938	9	11	7	27
1939	61	57	55	173
1940	6	8	7	21
1941	11	9	15	35
1942	3	5	2	10

It can readily be seen that even in years when the moths are very numerous, the larvae cause no serious destruction of seed.

Other insects* which have been consistently observed upon horse nettle are as follows:

<u>Name</u>	<u>Stage of Plant When Observed</u>			
Mealy bugs, <i>Pseudococcus</i> sp.	Entire life, especially young shoots			
Cucumber beetles or <i>Diabrotica</i> s, <i>Diabrotica duodecimpunctata</i> (F)	"	"	"	"
Flea beetles, <i>Epitrix fuscula</i> Gr.	"	"	"	"

*The author is indebted to Dr. Harold Gunderson, Extension Entomologist of Iowa State College and to Dr. C. F. W. Muesebeck and staff, U.S.D.A., Bureau of Entomology and Plant Quarantine for the identification of the insects.

<u>Name</u>	<u>Stage of Plant When Observed</u>			
Syrphus flies, Mesogramma marginata (Say)	Entire life, especially during flowering			
Scavenger or Dung flies, Campoproscopella sp.	"	"	"	"
Blow flies, Lucilia sericata (Mg.)	"	"	"	"
Leaf bug, Adelphocoris rapidus, Say	"	"	"	"
Clear winged moth, Conopia rileyana (Hy. Edw.)	"	"	"	"
Bumblebees, Bombus griseocollis (DeGeer)	"	"	"	"
" impatiens Cress	"	"	"	"
Long-tongue bee, Melissodes perplexa Cress	"	"	"	"

Eradication of Horse Nettle

Experiments on the eradication of horse nettle were conducted by summer fallowing, (hoeing), chemicals, and smother crops.

1. Summer fallowing (hoeing)

Young horse nettle plants from seed are very easily eradicated by cultivation during the first one or two months of their growth. This is shown in Tables 29 and 30.

Table 29
Eradication of One Month Old Seedlings by
Hoeing

Area A	Seed planted Apr. 15, 1940	Hoeed May 15, 1940 - none reappeared (out of 100)
Area B	Seed planted Apr. 15, 1940	Hoeed May 15, 1940 - none reappeared (out of 100)
Area C	Seed planted June 20, 1941	Hoeed July 21, 1941 - none reappeared (out of 100)
Area D	Seed planted June 20, 1941	Hoeed July 21, 1941 - none reappeared (out of 100)

Table 30
Eradication of Two Month Old Seedlings by
Hoeing

Area A	Seed planted Apr. 15, 1940	Hoeed June 15, 1940 - none reappeared (out of 100)
Area B	Seed planted Apr. 15, 1940	Hoeed June 15, 1940 - none reappeared (out of 100)
Area C	Seed planted June 20, 1941	Hoeed Aug. 24, 1941 - none reappeared (out of 100)
Area D	Seed planted June 20, 1941	Hoeed Aug. 24, 1941 - none reappeared (out of 100)

Plants more than two months old are capable of regenerating
new plants from roots as shown in Table 31.

Table 31
Eradication of Three Month Old Seedlings
by Hoeing

	Planting date	Hoeing date	Date of Reappearance	Date of Rehoeing	Reappearance
Area A	Apr. 15, 1940	July 17, 1940	July 27 (17%)	July 27, 1940	none
Area B	Apr. 15, 1940	July 17, 1940	July 27 (22%)	July 27, 1940	none
Area C	June 20, 1941	Sept. 17, 1941	Sept. 28 (37%)	Sept. 28, 1941	none
Area D	June 20, 1941	Sept. 17, 1941	Sept. 28 (54%)	Sept. 28, 1941	none

Four month old seedlings were killed by two successive hoeings or cultivations. Results of hoeings on four month old seedlings are shown in Table 32.

Table 32
Eradication of Four Month Old Seedlings by
Hoeing

	Seed planted	Hoeing date	Date of Reappearance	Date of Rehoeing	Reappearance
Area A	Apr. 15, 1940	Aug. 11, 1940	Aug. 19, 1940 (69 out of 100)	Aug. 19, 1940	none
Area B	Apr. 15, 1940	Aug. 11, 1940	Aug. 19, 1940 (52 out of 100)	Aug. 19, 1940	none
Area C	Apr. 15, 1940	Aug. 11, 1940	Aug. 19, 1940 (77 out of 100)	Aug. 19, 1940	none

One year old roots are capable of extensive shoot regeneration. Seeds of horse nettle were planted in the spring of 1940 and 1941 in a cultivated area at Ames. The plants were allowed to grow unmolested during the entire first year. Typical one year old plants are shown in Figure 11, and typical one year old roots are shown in Figure 10. Eradication measures were started the second year. All shoots which were hoed off were removed from the area. The results are shown in Table 33.

Table 33

Eradication of One Year Old Plants from
Roots

Area A Seed Planted April 15, 1940. Eradication of One Year Old Roots in 1941.

<u>Treatment</u>	<u>Date</u>	<u>Date of Reappearance</u>
Plowed	April 22	May 12
Hoed	May 14	May 24
Hoed	May 28	June 8
Hoed	June 12	June 19
Hoed	June 23	July 2
Hoed	July 5	August 7
Hoed	August 11	None reappeared
Hoed	September 17	None reappeared

Area B Seed Planted May 2, 1941. Eradication of One Year Old Roots in 1942.

<u>Treatment</u>	<u>Date</u>	<u>Date of Reappearance</u>
Plowed	April 15	April 26
Hoed	April 28	May 6
Hoed	May 7	May 15
Hoed	May 18	June 8
Hoed	June 12	July 12
Hoed	July 14	August 28
Hoed	August 31	None reappeared
Plowed	September 30	None reappeared

Table 33 shows that even one year old plants are very difficult to kill. This observation has erroneously convinced many farmers that horse nettle plants cannot be killed out after they become established. Plants from seed are easily killed during the first two months (Table 30). After two months regenerative shoots appear from the hoed off plants as is shown in Table 31.

Established roots are very difficult to eradicate because they have remarkable ability to produce shoots if the above ground portion of the plant is destroyed. Table 34 shows the number of days required for established roots to produce new shoots after the tops were cut off at about a 2-3 inch depth, as in normal cultivating operations.

Table 34

Days Required to Produce New Shoots from Old
Roots - 1940-1942 inclusive

	Shoots Hoed Off	New Shoots Reappeared	Interval
1940	May 15	May 22	7 days
	May 25	June 4	10 days
	June 15	June 22	7 days
	July 14	July 20	7 days
	August 10	August 18	8 days
1941	June 1	June 8	7 days
	July 5	July 14	9 days

Table 34 (cont.)

	Shoots Hoed Off	New Shoots Reappeared	Interval
1941	August 9	August 19	10 days
	August 20	August 30	10 days
1942	May 13	May 19	6 days
	June 7	June 21 (cold wet weather)	14 days
	June 23	July 1	8 days
	July 15	July 22	7 days
	August 15	August 23	8 days
	September 1	September 11	10 days

The plants cut on June 7, 1942, which were partially covered with soil by cultivation and had a period of wet weather, reestablished themselves and produced seed. This condition has also been observed repeatedly in farmers' fields in wet soils and wet years when cultivation served to spread rather than eradicate horse nettle.

Table 33 has shown that complete eradication of one year old plants requires from 6-8 cultivations. On large, old, well established patches, limited experiments (11 separate 1 square rod areas in three locations) indicate that weekly cultivation for 20 weeks from May through September, repeated for two seasons, accomplished eradication of established plants.

Shoots from roots usually appeared in from 5-7 days after cultivations. Fewer than ten cultivations per season enable the plant to survive indefinitely.

Another experiment (6 separate 1 sq. rod areas in 2 locations) demonstrated that the time interval between hoeings and cultivations may be lengthened from one week to two weeks and still result in effective eradication. Hoeing was done at a depth of 1-3 inches. The practical application of these experiments is that cultivation intervals need not keep the "ground black", but may allow some top growth, thus reducing the cost of labor. Often 2-3 inches of top growth was present at the time of cultivations. Further experiments may indicate possible lengthening of the cultivation intervals.

Close scything or mowing is not as effective as hoeing even if close cutting is done regularly. On 4 separate 1 square rod areas in two locations where a total of 50 close scythings were made in 1936 and 1937, 57 plants reappeared from roots in the spring of 1938. On plants cut off so that aerial axillary buds remained, axillary growth occurred in 3-4 days.

2. Eradication by means of chemicals

For small infestations of horse nettle, or for scattered plants on large areas, individual plant treatment was tested. The following experiment was designed to determine the best

Table 35

Individual Plant Treatment with Various Substances

Material and amount used per plant	: 1st : 2nd : 3rd : 4th : 5th				
	:treatment: 7-27-38	:treatment: 10-4-38	:treatment: 6-30-39	:treatment: 9-2-39	:treatment: 7-2-40
Sodium chlorate, one teaspoon per cut plant	Area A 103	41	3	0	0
	Area B 81	27	11	0	0
	Area C 106	38	7	1	0
	Area D 41	11	2	0	0
Attlacide, one teaspoon per cut plant	Area A 104	97	21	1	0
	Area B 112	114	63	11	0
	Area C 97	91	45	19	0
	Area D 84	61	33	24	0
Salt, one teaspoon per cut plant	Area A 116	109	87	34	4
	Area B 77	69	71	44	11
	Area C 81	72	68	31	2
Kerosene, one tablespoon per cut plant	Area A 96	92	88	83	71
	Area B 90	83	87	78	62
	Area C 121	103	109	89	91
Lewis Lye, one table- spoon per cut plant	Area A 103	81	42	11	2
	Area B 76	54	31	9	4
	Area C 82	36	44	23	17
Hoed only (one inch below surface)	Area A 154	241	213	161	141
	Area B 97	102	88	92	91
	Area C 117	124	128	114	74
Check plot (no treatment)	Area A 114	118	111	119	126

methods and materials for treating individual plants. All plants were cut about one inch below ground line, the killing agents placed directly on the root and the soil replaced. The same materials and amount were used on each retreatment as were used in the original treatment. After the first treatment, the number of plants treated indicates the number of survivors following the preceding treatment. Table 35 summarizes the results of five separate treatments.

It is obvious that individual plant treatment with chemicals is practicable only on small areas, or on large areas where the plants are very scattered, and where the total number of plants involved is small. Of the materials tested, the chlorates (sodium chlorate and Atlacide), when used for spot treatments, gave better results than similar applications of salt, Lewis lye, kerosene, or hoeing.

In contrast to eradicating well established areas of horse nettle by means of the spot treatment, it seemed desirable to determine the effect of various chemicals on one year old plants. In this experiment, plants were grown from seed planted June 1, 1939. Missing plants in the row were supplied by seedlings grown in the greenhouse and transplanted to the row. The plants were thinned and cultivated until October 14, 1939, when they were cut one inch below the surface of the

ground, treated with one teaspoonful of the material per plant, after which the soil was replaced. The results are shown in Table 36.

Table 36
Effect of Various Substances on One Year Old
Horse Nettle Plants
(1 teaspoonful per plant)

Chemical	No. of plants treated	No. of plants surviving
Sodium chlorate	10	0
Atlacide	12	0
Check	11	11
Crankcase oil	10	10
Kerosene	10	9
Lewis lye	10	3
Salt	12	4
Bentonite	9	9

Eradication was found to be most effective with sodium chlorate or atlacide. Examination of such one year old plants indicates that they consist primarily of a single vertical root, with very few horizontal roots.

Areas beyond the scope of individual plant treatment may be controlled by spraying with weed-killing chemicals. In the following experiments spraying was done with a three gallon knapsack pressure sprayer. Dates for spraying were chosen when high soil and air moisture conditions prevailed,

and when dew and general cool weather conditions prevailed. All plots had heavy infestation. Six quadrat counts showed an average of 23 plants per meter quadrat and all plants were blooming at the time of the first spraying. All plants were thoroughly wetted with the solution. Table 37 summarizes the results of spraying over a two year period.

In all cases spraying with chlorates gave better results than bentonite, kerosene, or crankcase oil. Bentonite did not kill the foliage of the sprayed plants. Crankcase oil and kerosene did kill the tops of the plants, but additional growth was so rapid and profuse that apparently very little damage was done to the plant. The new growth often came from immediately below the ground line, indicating lack of translocation of the herbicide.

The data in Table 37 and other evidence indicates that satisfactory killing can be obtained by applications of sodium chlorate or Atlacide at the rate of one pound to one gallon of water applied with a pressure sprayer, when optimum weather and soil moisture conditions prevail, and when treatment is applied early in the season when the plants are in bloom. Heavy infestations require at least two gallons of spraying solution per square rod to wet all plants thoroughly. Two sprayings, and often three, are required to eradicate an infestation. Best results are obtained when initial spraying is done in June, with a follow-up in September and again in the following June

Table 37

Effect of Spraying on Horse Nettle with Various Substances

Material and concentration		lbs. chemical	gal. water	Substrate	Total no. of sq. rds. in plot	1st spray	% kill	2nd spray	% kill	3rd spray	% kill
Sodium chlorate	2	2		Blue grass pasture	2	6-25-36	75	9-7-36	80	6-20-37	98
Sodium chlorate	6	6		Blue grass pasture	3	6-27-37	85	9-9-37	95	6-26-38	100
Sodium chlorate	1	1		Blue grass pasture	1	7-16-37	60	9-27-37	75	7-20-38	90
Sodium chlorate	2	2		Blue grass pasture	1	6-30-37	82	9-6-37	90	6-22-38	100
Sodium chlorate	2	2		Annual weeds	1	6-21-38	85	9-13-38	95	6-26-39	100
Sodium chlorate	2	2		Annual weeds	1	7-15-39	65	9-4-39	75	6-17-40	97
Sodium chlorate	4	4		Clover after oats	2	6-29-39	85	9-7-39	100	7-7-40	100
Atlatide	6	6		Blue grass pasture	3	6-38-37	80	9-10-37	95	6-26-38	100
Atlatide	2	2		Blue grass pasture	1	7-14-37	60	9-27-37	80	6-29-38	95
Atlatide	2	2		Clover after	2	6-29-39	85	9-8-39	99	7-7-40	100
Bentonite	1	1		Annual weeds	1	6-15-41	0	9-3-41	0	6-26-42	0
Crank case oil	1 gal. to 1 sq. rd.			Annual weeds	1	6-15-41	heavy growth	9-3-41	heavy growth	6-26-42	heavy growth
Kerosene	1 gal. to 1 sq. rd.			Annual weeds	1	6-15-41	"	9-3-41	"	6-26-42	"

if necessary. This has consistently given better control than initial fall sprayings followed by June and September retreatments.

Good control was also obtained by using the dry chemical treatment in the fall. On uniform, heavy infestations, sodium chlorate and Atlacide were applied by hand, as evenly as possible, to the surface of the ground. Tetrachlorethane and larvacide were applied with a special injector manufactured for that purpose. The land was undisturbed throughout the tests in all cases. Results of such treatments are given in Table 38.

Table 38
Effect of Fall Treatment with Chemicals on
Horse Nettle

Material and amount used	Date of Treatment	No. of plants surviving per sq. rd. (6-30-38)
Sodium chlorate 2 lbs. per sq. rd.	9/20/37	34
Sodium chlorate 3 lbs. per sq. rd.	9/20/37	14
Sodium chlorate 4 lbs. per sq. rd.	9/20/37	10
Sodium chlorate 5 lbs. per sq. rd.	9/20/37	7
Atlacide 2 lbs. per sq. rd.	9/19/37	17
Atlacide 3 lbs. per sq. rd.	9/19/37	16
Atlacide 4 lbs. per sq. rd.	9/19/37	24
Atlacide 5 lbs. per sq. rd.	9/19/37	13
Check heavy growth throughout plot		
Chloripicrin 2 oz. per 10 in. staggered 6 in. hole	8/10/37	39
Tetachlorethane 2 oz. per 10 in. staggered 6 in. hole	8/10/37	2

While dry chlorates used in the fall are effective agents for killing horse nettle, the method is more expensive than spraying. At least two treatments, the second of which may be spot treatment, are necessary. Tetrachlorethane is much more effective than larvacide.

An important factor in chemical weed eradication is the residual effect certain chemicals have on the soil. To determine after effects of chemicals on the soil, three chemicals were applied, both in spray and dry form in the fall (8/2/36). The land was spring plowed, disced and harrowed once. Corn was planted and cultivated three times using shovel plows. The corn was husked and weighed October 29, 1937. Results are shown in Table 39.

Table 39
Effect of Chemical Weed Killers on Following
Season's Crops (Corn)

Chemical	Amt. used per sq. rd.	No. of plants per sq. ft. quadrat (Av. of 4 quad.)	Corn yield in lbs. per 25 hills
Sodium chlorate (dry)	3 lbs.	10.2	.8
Sodium chlorate (dry)	3 lbs.	9.5	.6
Sodium chlorate (spray)	3 lbs.	12.5	1.0
Sodium chlorate (spray)	3 lbs.	10.7	1.5
Atlacide (dry)	3 lbs.	22.7	4.5
Atlacide (dry)	3 lbs.	19.2	4.9
Atlacide (spray)	3 lbs.	28.0	3.3
Atlacide (spray)	3 lbs.	27.0	3.7
Sodium Thiocyanate (dry)	3	66.2	37.0
Sodium Thiocyanate (dry)	3	48.7	39.3
Sodium Thiocyanate (spray)	3	68.5	36.5
Sodium Thiocyanate (spray)	3	59.0	38.2
Check	No treatment	24.5	41.3
Check	No treatment	20.7	42.4

While the chlorates are the best weed killers, they also have the most adverse effect on the soil. The horse nettle plants in the sodium thiocyanate plots were larger and more numerous than in the untreated plots.

The following experiment furnishes some evidence of the effect of heavy infestations on corn yields. Areas where soil moisture, drainage, contour, and fertility were identical as far as could be observed were chosen for this experiment. The areas were staked out about a week after the corn had been cultivated the third time. The plots were divided in half, one half being heavily infested with horse nettle, the other half being clean. The corn was husked on November 3, 1937 and weighed immediately. Results are shown in Table 40.

Table 40

Loss of Crop (Corn) Due to Horse Nettle Infection

Horse nettle plants per 9 sq. ft. quadrat (average of 4 quadrats)	Corn yield in lbs. per 25 hills	Total yield of corn per 100 hills
Area 1 (Level land)		
27.2	52.3	
23.5	57.7	214.8
27.0	51.5	
25.5	53.3	
none	53.7	
none	59.0	218.6
none	54.7	
none	51.2	
Area B (Low land)		
57.7	44.3	
54.2	42.6	171.8
52.7	41.7	
42.7	43.2	
none	43.4	
none	42.8	175.3
none	45.0	
none	44.1	
Area C (Level land)		
39.5	53.6	
32.0	56.1	212.4
40.0	49.9	
35.0	52.8	
none	57.1	
none	55.2	219.4
none	51.4	
none	55.7	

It appears from these limited observations that horse nettle causes marked reduction in crop yields.

To determine the toxicity of various chemicals to horse nettle seed in the soil, seeds were planted one inch in depth,

in six inch greenhouse pots, half of them watered and left overnight. The treatments on both dry and wet soil were made the following day, the pots covered with waxed paper fastened with a rubber band and left for two days. Results are shown in Table 41.

Table 41
Germinating Horse Nettle Seeds Following Soil
Treatment with Chemicals (70° F.)

Sample No.	Treatment	% Germination per 400 seeds (4 lots of 100 seeds each)
1	Chloropierin 2 drops dry soil	8.0
2	" 2 drops wet soil	45.0
3	" 4 " dry "	0.0
4	" " wet "	0.0
5	" 6 " dry "	0.0
6	" " wet "	0.0
7	" 8 " dry "	0.0
8	" " wet "	1.0
9	" 10 " dry "	0.0
10	" " wet "	0.0
11(check)	No treatment dry soil	73.0
12(check)	" " wet "	64.0
13	Sodium chlorate $\frac{1}{2}$ gram per 15 cc. water	48.0
14	" " $\frac{1}{4}$ " " " " "	52.0
15	" " $\frac{1}{8}$ " " " " "	21.0
16	" " 1 " " " " "	29.0
17	" " 2 " " " " "	31.0
18(check)	No treatment dry soil	69.1
19(check)	Sodium chlorate no treatment dry soil	72.3
20	Atlacide $\frac{1}{2}$ gram in 15 cc. water	36.0
21	" " $\frac{1}{4}$ " " " " "	33.0
22	" " $\frac{1}{8}$ " " " " "	60.0
23	" " 1 " " " " "	12.0
24	" " 2 " " " " "	16.0
25(check)	No treatment	71.0
26	Carbon bisulphide 2 drops dry soil	47.0
27	" " " wet "	75.0
28	" " 4 " dry "	78.0
29	" " " wet "	68.0
30	" " 6 " dry "	43.0
31	" " " wet "	90.0
32	" " 8 " dry "	54.0

(con'd)

Table 41 (con'd)

Sample No.	Treatment				% Germination per 400 seeds (4 lots of 100 seeds each)
33	Carbon bisulphide	8 drops	wet	soil	66.0
34	"	10 "	dry	"	59.0
35	"	10 "	wet	"	52.0
36 (check)	No treatment		dry	soil	75.0
37 (check)	"		wet	soil	74.0

In areas where horse nettle has been eradicated, the problem of seeds in the soil is ever present. The chlorates are not effective for killing these seeds. Of the materials tested chloropicrin proved to be the most effective.

Chemical treatment can be definitely recommended for small areas or scattered plants, but it is too costly on large areas. Large, heavily infested areas must be eradicated by cultural practices which permit continued income from the land.

Two experiments were performed to test the effectiveness of weed burning torches in the eradication of horse nettle. The first experiment was designed to test the effectiveness of this torch for destroying the seeds in the berries in the fall. Plants bearing mature berries were subjected to the flame of an Aeroil Weed Burner Torch (1800°F.--2000°F. acc. of Mfr.) on October 11, 1936 for varying lengths of time. The scorched berries were then picked and stored for two months at room temperature in the laboratory. The berries were then crushed and the seeds germinated (35° C. constant for 28 days.) The

results obtained are shown in Table 42.

Table 42
Effect of Aeroil Burner Torch on Horse Nettle
Seed Germination

Sample No.	Time exposed to flame (in seconds)	% germination per 1000 seeds (10 lots of 100 seeds each)
1	5	91.5
2	10	89.5
3	15	88.75
4	20	75.0
5	25	22.0
6	30	23.25
7	35	0.0
8	40	0.0
9	45	0.0
10	50	0.0
11	55	0.0
12	60	0.0
13 (check)	no treatment	85.25

Another experiment was made on another area where two square rod plots were burned weekly from June to October (total of 16 burnings) and where an additional two square rod plots were burned every two weeks (total of 8 burnings). This treatment failed to eradicate horse nettle, but the lowered vigor of the plants in the burned plots was obvious the following spring (1937). Although the cost of materials used for burning is not as great as the cost of herbicides, the labor cost is such that even on small areas the torch is not as economical as chemical treatment. Destruction of seeds is also impractical because a long interval is required to kill the seeds in the pulpy berries.

Results with 2-4 D (2-4 Dichlorophenoxyacetic acid) sprays.

Six square rod plots heavily infested with horse nettle were sprayed with three different brands of 2-4-D. (Weedone 1:60, Dow Weed Killer A510 1:100, and Weedicide 1 oz: 1 gal.) The plants were sprayed July 14, 1945. The temperature at time of application and four hours thereafter ranged from 77° - 86°F. The maximum temperature for three days following treatment was 73°, 89°, and 84°F. At the end of one week many plants were markedly deformed. At the end of two weeks many of the younger, more succulent plants were beginning to dry up and die. No difference was apparent between the three compounds used. Some plants, even though markedly deformed, continued somewhat green until frost. Examination of some of the roots on October 29 disclosed many dead vertical roots and some dead horizontal roots. However, on October 29, many roots, especially the deeper portions of the vertical roots, still appeared more or less normal macroscopically. Some of the roots were abnormally large in diameter.

It appears that the "hormone" or "growth regulating" sprays need to be applied earlier in the season when the plants are in more succulent, active growing condition. It cannot be stated at this time how many follow-up treatments will be necessary. Final evaluation of the 2-4 D treatments involving the three above mentioned materials will not be possible until later in the season of 1946 when total amount of regrowth

is ascertained. While some regrowth from roots is becoming apparent, there appears to be at this time, a marked reduction in stand and vigor of the horse nettle plants.

3. Use of smother crops

On large, uniformly and heavily infested areas, where the previously described treatments are not practicable, and where it is necessary to secure income from the land, some cultural method of control is desirable. Cooperative experiments with farmers using such methods are difficult to conduct because experiments must extend over several years and because check plots are needed. In the limited experiments conducted under these handicaps, counts of random square meter quadrats were made each year, as an indication of the progress of eradication.

A twenty acre field (Boone County) badly infested with horse nettle was seeded to alfalfa (15 lbs. to acre), with oats in the spring of 1936, following corn. The oats were removed as grain as early as possible. The alfalfa maintained a good stand throughout the experiment. Twenty-five random quadrat counts were made on this area in 1936. Results are shown in Table 43.

Table 43

Effect of Cropping with Alfalfa on Eradication
of Horse Nettle

Year	Cuttings	Number of quadrats	Total number of plants in quadrats	Average number of plants per quadrat
1936		25	88	3.52
1937	3	25	93	3.72 (Plants less vigor- ous)
1938	3	25	53	2.12
1939	2	25	12	.45 (Weak and spindly plants)
1940	1	25	0	0.0

In another 11 acre field (Sac County) alfalfa was fall seeded at the rate of 15 lbs. to the acre. First quadrat counts made at random in the spring of 1937. Summarized results are shown in Table 44. Another experiment is recorded in Table 45.

Table 44

Effect of Cropping (Alfalfa) on Horse
Nettle

Year	No. Cuttings	Number of quadrats	Total number of plants in quadrats	Average number of plants per quadrat
1937	3	25	105	4.2
1938	2	25	81	3.24
1939	2	25	26	1.04
1940	1	25	2	.08

Table 45

Effect of Cropping (Alfalfa) on Horse
Nettle

Year	No. Cuttings	Number of quadrats	Total number of plants in quadrats	Average number of plants per quadrat
1937	2	25	116	4.64
1938	2	25	62	6.48
1939	2	25	41	1.64
1940	1	25	4	.16

Two other cooperative experiments with alfalfa were begun. After showing considerable reduction in the horse nettle stand, the experiments were discontinued because the stand of alfalfa was lost by winter-killing.

From limited trials recorded above and from extensive observations 4-5 years of alfalfa, with frequent cutting, is necessary to kill out established areas of horse nettle. The alfalfa stand must be heavy to act as a good smother crop (Fig. 6).

One experiment using rye combined with summer fallow was undertaken to ascertain the value of this method of eradicating horse nettle. An 18 acre field in Sac County was found to be infested with horse nettle when eradication measures were begun in the summer of 1937. Twenty quadrat counts made in the oat stubble showed an average of 5.25 horse nettle plants per quadrat. The oat stubble was plowed, disced twice when the horse nettles reappeared, and seeded to rye in September. The rye crop was removed as a cash crop, the land plowed, disced four times and reseeded to rye. The second cash crop of rye was removed in 1939, the land again plowed and disced four times when the horse nettle plants reappeared. One half the area was then sown to alfalfa.

The other half of the original rye area was planted to check corn in 1940. The corn was cultivated three times. In September 1940, digging revealed that most of the surviving horse nettle plants were from seed, but many came from old roots.

The summarized results of rye-summer fallow as a smother crop of horse nettle is shown in Table 46.

Table 46

Results of Summer Fallow-Rye on Horse Nettle

Year	Number of quadrats	Total number of plants in quadrats	Plants per quadrat
1937	20	105	5.25
1938	20	48	2.4
1939	20	13	.65
1940	20 (alfalfa)	0	0.0
1940	20 (corn)	65	3.25

Alfalfa appears to be the logical follow up crop to use after the horse nettle plants have been weakened by other methods. It combats seedlings as well as weakened plants which reappear from old roots.

The use of Sudan grass was tested on a heavily and uniformly infected six acre field in Green County. During the growing season of 1937 when the area was in corn, a count of 3.45 horse nettle plants was obtained. The following spring the area was plowed, disced twice at 14 day intervals when the horse nettle appeared, and Sudan grass was broadcast at the rate of 20 lbs. per acre. Horse nettle growth in the area was heavy, but spindly as well as of a very light green color. It was impossible to make quadrat counts while the Sudan grass was on the area. The crop (far removed from buildings) was never harvested, allowed to go down and burned off in the spring of 1939. Then the area was plowed, disced twice when horse

nettles reappeared and replanted to Sudan grass as before. Horse nettle growth appeared spindly and sickly. The crop was again allowed to go down, was burned off the following spring, the land plowed, a seed bed prepared and corn planted upon the insistence of the landowner in the spring of 1940. A quadrat count in July of 1940, after the corn had been "laid by", showed .45 horse nettle plants per quadrat, a distinct reduction in the number of plants over when the smother crop program was inaugurated. The land should have been retained in smother crops or planted to alfalfa instead of corn. The summarized results of this experiment are shown in Table 47.

Table 47

Effect of a Smother Crop (Sudan Grass) on Horse Nettle

Year	Cultivations	No. quadrats	Number of plants in quadrats	Number of plants in quadrats
1937	Spring plow, 3 cultiv. in corn	20	69	3.45
1938	Spring plowed, disced twice	No counts	-	-
1939	Spring plowed, (burned) disced twice	No counts	-	-
1940	Spring plowed, (burned) 3 cultiv. in corn	20	9	.45

Quadrat counts were made in pastures and hay lots where horse nettle were thoroughly established. Results of quadrat counts in infested pastures and hog lots are shown in Table 48.

Table 48
Effect of Pasturing on Horse Nettle

Year	Number of Plants per Quadrat (Av. number of 6 quadrats)
Area A (hogs)	
1936	13.1
1937	12.7
1938	16.6
1939	20.4
1940	14.1
Area B (hogs and cattle)	
1936	25.6
1937	31.0
1938	30.1
1939	24.8
1940	27.1
Area C (cattle)	
1936	33.3
1937	31.8
1938	32.0
1939	37.5
1940	36.5

Livestock does not eat the plant readily enough to do it major damage. Observations over a 5 year period indicate that pasturing with hogs alone, or cattle alone, or cattle-hog combinations, does not eradicate horse nettle. In all areas studied, the plants produced seed. Very seldom was it possible

to find plants which had been eaten off. Broken and injured plants, if not injured too severely, invariably produced sufficient callus tissue and survived the season. Two heavily grazed pastures and one hog lot under observation for five years showed that the weed increased its distribution in all areas.

DISCUSSION

Horse nettle has not been officially reported from five counties in the state but it is probable that it already occurs in every Iowa county.

The claim that horse nettle freezes back to a depth of eighteen inches in the soil every year is not substantiated by the present investigation. New shoots from perennial roots (Figs. 5 and 8) have consistently been found to occur at or slightly below the ground line every year that the plant has been under observation. While the roots winterkilled readily upon exposure or quick freezing and thawing in experiments, this is not the case when they are adequately protected by soil in their natural condition.

The histological ontogeny is in most major respects in close agreement with descriptions of other solanaceous plants such as potato as reported by Artschwager (3) or tomato as reported by Smith (93). Some floral abnormalities were observed. These are pictured in Figures 12 and 13.

Protophloem has been reported to differentiate before protoxylem. The present study indicates that protophloem in the stem arises more or less simultaneously with the protoxylem. Protoxylem elements are distinguished quite early by their

secondary wall thickenings. Protophloem cells are distinguishable from the procambium only by location, slightly larger size, and more irregular shape.

The ontogeny of the root corresponds in many respects quite closely to that of the pear as described by Esau (39). The roots serve as the main overwintering organs of the plant. Even half inch pieces of roots are consistently able to reproduce the plant. It follows that no cultivating device can cut all roots into small enough pieces to eliminate contamination of clean areas by transplanted roots. Many roots are undoubtedly destroyed by cultivation but unless hot sun, dry wind, or dry soil prevail, cultivation may actually serve to spread, rather than eliminate horse nettle infestations.

The abundant shoot formation shown in histological studies is verified by field observations. The extensive callus formation noted in the histological study was also frequently encountered in the field where very severely injured plants were found to be able to complete their entire life cycle.

Pammel (80) stated that sheep, cattle, or horses do not eat horse nettle, but during the present study horse nettle plants in sheep pastures were frequently observed to be stripped of berries. Whether the seeds of horse nettle are spread in this manner was not ascertained. No study was made to ascertain to what extent seed is distributed by birds (110).

In seed germination a constant temperature of 35° C. gave optimum results. However some alternating temperatures also gave satisfactory germination. Germination tests show clearly that there is a lack of dormancy in the seed and that after ripening does occur. This latter observation has practical application in that farmers frequently mow horse nettle plants after sizeable berries have appeared. Usually these plants are left in the field and perhaps frequently ripen.

The extensive shoot regeneration which occurs in this plant has often erroneously convinced many farmers that the plant cannot be eradicated. Moreover this study has definitely shown that plants may arise from seed in the spring and bloom by fall. Thus even after a stand of plants has been killed out, seed is often still present.

Horse nettle plants usually make their appearance late in the spring but they grow very rapidly after emerging. Histological sections disclose a periodic disappearance of starch in the roots with the resumption of above ground activity. The first frost stops all above ground growth in the fall.

Many variables enter into horse nettle eradication by means of chemicals as well as by smother crops. Physiological strains of species probably differ in responses. Temperature, moisture conditions, and stage of the plant, as well as location, certainly influence chemical weed eradication. The topography and condition of the soil influence the weed as well as the smother crop

which might be used. Often conditions favorable for eradication are beyond the control of the experimenter. Since so many variables are involved, different results are often secured under seemingly identical conditions. At the present time, each chemical has its own optimum range of usefulness. The variables involved with present chemicals plus the seedling problem which occurs after eradication is seemingly complete, are the two major problems involved in promoting a good weed control program at the present time.

SUMMARY

1. A study was made of the biology of horse nettle, including distribution, developmental morphology, life history, and control methods.
2. Horse nettle was found to occur in 94 counties in Iowa and is much more serious in southern Iowa than farther north.
3. The primary histogens of the stem apex consist of tunica and corpus.
4. Leaf formation is initiated in the corpus involving at least three layers of cells; the lamina enlarges by the activity of marginal meristems, and the permanent tissues are evident in the second leaf from the apex.
5. Glandular and stellate hairs are derived from epidermal cells. Spines arise as a result of anti and periclinal divisions of epidermis and outer cortical regions.
6. The vascular system is initiated approximately 130 microns from the growing point and consists of five procambium strands.
7. Interfascicular cambium develops by the reactivation of primary ray cells.
8. Periderm formation in the stem is brought about by periclinal division of epidermal cells.

9. Underground stems arise adventitiously from either vertical or horizontal roots by reactivation in the secondary phloem.
10. Underground stems are histologically similar to aerial stems but lack spines, epidermal hairs, and chlorophyll.
11. The primary meristem of the radicle is an open type of promeristem which differentiates into three histogens, dermatogen, periblem, and plerome.
12. Horizontal roots arise endogenously in the pericycle, and their initiation, development, and mature structure corresponds in all respects to vertical roots.
13. At the end of the second week after emergence, vegetative shoots were found to have floral primordia.
14. Differentiation of floral parts takes place acropetally.
15. The monoploid chromosome number is 12 and the diploid number is 24.
16. The megasporocyte produces a linear tetrad of megaspores; the chalazal megaspore gives rise to the female gametophyte which consists of the egg, two synergids, two polar nuclei, and three antipodal nuclei.
17. In Iowa horse nettle blooms continuously from May or June until frost.
18. Pollen tubes produced by germinating pollen frequently attained lengths 40 times greater than the pollen diameter.
19. Viable seed may be produced either by self or cross pollination. Both types of pollination may occur in the field.

20. The primary endosperm nucleus divides in advance of the zygote and the rapidly growing endosperm envelops the embryo.
21. Histogens may be distinguished prior to initiation of organs in the embryo.
22. A constant temperature of 35° C. is optimum for seed germination.
23. Germination tests disclose that after ripening occurs; that no dormancy occurs in roots or seed and that the seeds may remain viable for several years under laboratory storage.
24. The most prominent pathogen found on horse nettle is mildew, Erysiphe cichoracearum D. C. Other diseases observed were rust, Puccinia tubulosa (Pat. and Gaill) Arthur and Fromme, an unidentified blossom end rot, and a "damping off" disease.
25. The most prominent insects found on horse nettle include the potato flea beetle, Epitrix cucumeris Harris, the Colorado potato beetle, Leptinotarsa decemlineata Say, and a gall moth, Gnorimoschema lavernella Chambers. Several other insects were also consistently observed on the plant.
26. Seedlings which are two months old are easily eradicated by one hoeing or cultivation. Older seedlings regenerate new plants after cultivation.

27. Perennial roots do not consistently winterkill to any appreciable depth every year. Shoots from perennial roots have seven macroscopic leaves at time of emergence from the ground.
28. Roots which are one year old are capable of extensive shoot regeneration, usually in from 7-10 days. Six to eight cultivations are usually necessary to kill one year old plants. Close mowing is not as effective as cultivation. Fewer than ten cultivations per season enable the plant to survive indefinitely.
29. Eradication of small numbers of well established horse nettle plants is best accomplished by individual spot treatment with sodium chlorate or Atlacide. Three or four treatments are usually necessary. Dry application of sodium chlorate or Atlacide over large areas is effective, but more than one treatment is required.
30. Seedlings are easily killed any time during their first year by one spot treatment of sodium chlorate or Atlacide.
31. For small areas, spraying with sodium chlorate or Atlacide gave best results. Usually two or more sprayings are required.
32. Tetrachlorethane proved more effective than larvacide for eradicating horse nettle through soil injection.
33. Application of sodium chlorate, either in spray or dry form proved more detrimental to the subsequent crop (corn)

than did Atlacide or sodium thiocyanate.

34. Chloropicrin holds promise of killing horse nettle seeds in the soil. It is too costly to use on large areas.
35. Weed burning torches proved less effective in controlling horse nettle than chemicals.
36. Preparations containing 2,4-dichlorophenoxyacetic acid hold promise of eradicating horse nettle. More than one application is required.
37. Alfalfa is effective as a smother crop for weakening and eventually eradicating horse nettle on large areas. A good stand must be maintained over a 4-5 year period to be effective.
38. Two seasons of rye-summer fallow combination followed by alfalfa was effective in eradicating horse nettle.
39. Sudan grass proved effective in weakening horse nettle.
40. Pasturing with hogs or cattle, or cattle hog combinations proved ineffective in controlling horse nettle.

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ACKNOWLEDGMENT

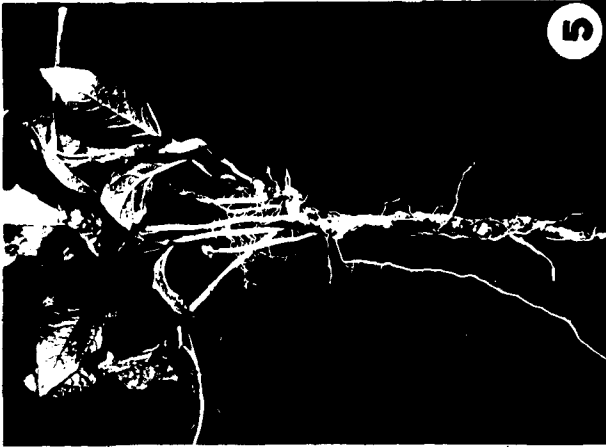
The author wishes to express his sincerest appreciation to Dr. J. E. Sass and Dr. R. H. Porter for encouragement and helpful suggestions during the entire course of this study.

FIGURES

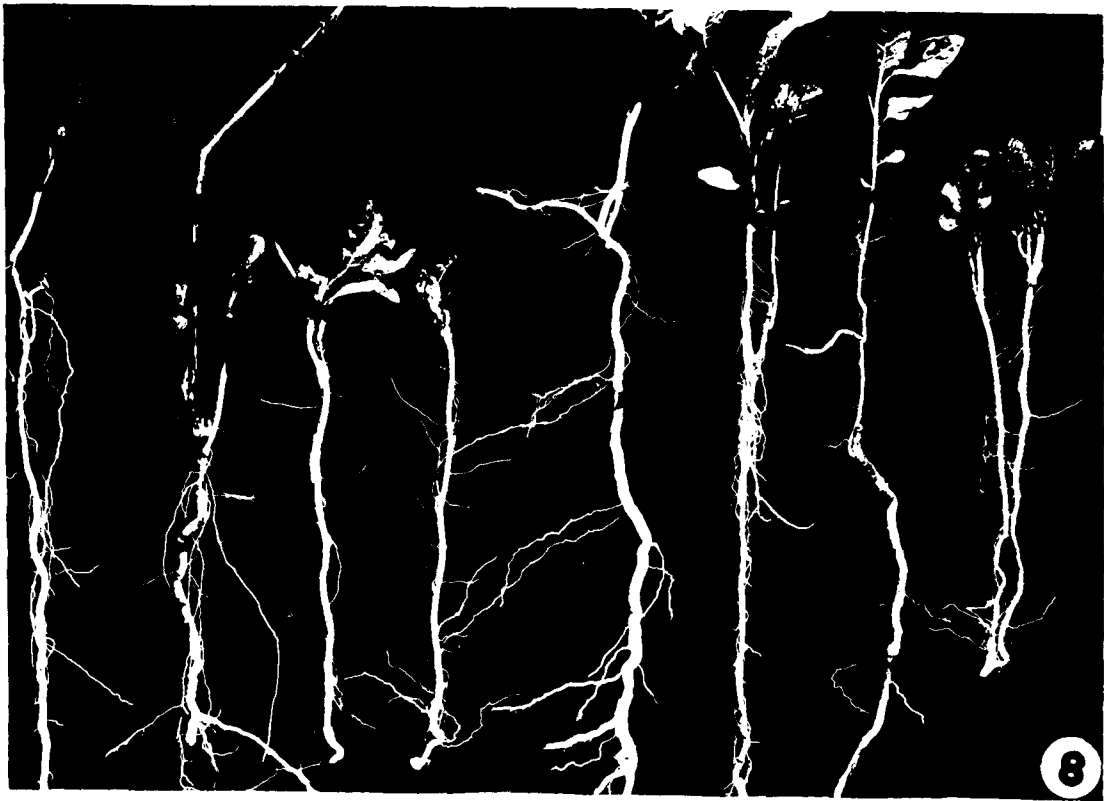
- Fig. 1. Defoliated horse nettle plant gathered in January, showing persistence of spines and berries on the plants.
- Fig. 2. Horse nettle in early summer, showing spines and flowers.
- Fig. 3. Leaves of horse nettle showing variations in outline and severity of mildew infection.



- Fig. 4. One year old horse nettle plant grown from seed.
- Fig. 5. Shoots of horse nettle arising from vertical roots. Origin of shoots is only 1-2 inches below ground line.
- Fig. 6. Smothering effect of alfalfa; spindly horse nettle in third year of alfalfa cover.
- Fig. 7. Origin of horse nettle shoots from horizontal roots. The horizontal root in this case is only $3\frac{1}{2}$ inches deep.



- Fig. 8. Origin of shoots from vertical roots. In the second shoot from the left, the old remains of last year's stem is still present; young shoots arise approximately at the ground line.
- Fig. 9. Insect damage on horse nettle leaves caused by flea beetle, Epitrix cucumeris Harris and Colorado potato beetle, Leptinotarsa decemlineata Say.



- Fig. 10. One and two year old roots of horse nettle. Note absence of lateral roots on one year old plants and presence on two year old plants.
- Fig. 11. One year old roots in their second year of growth. Note formation of laterals. The two roots on the left are the same roots shown on the left in Fig. 10 photographed 3 months later.
- Fig. 12. Flower containing two complete sets of floral organs.
- Fig. 13. Abnormal fruit of horse nettle, developed from type of flower shown in Fig. 12.

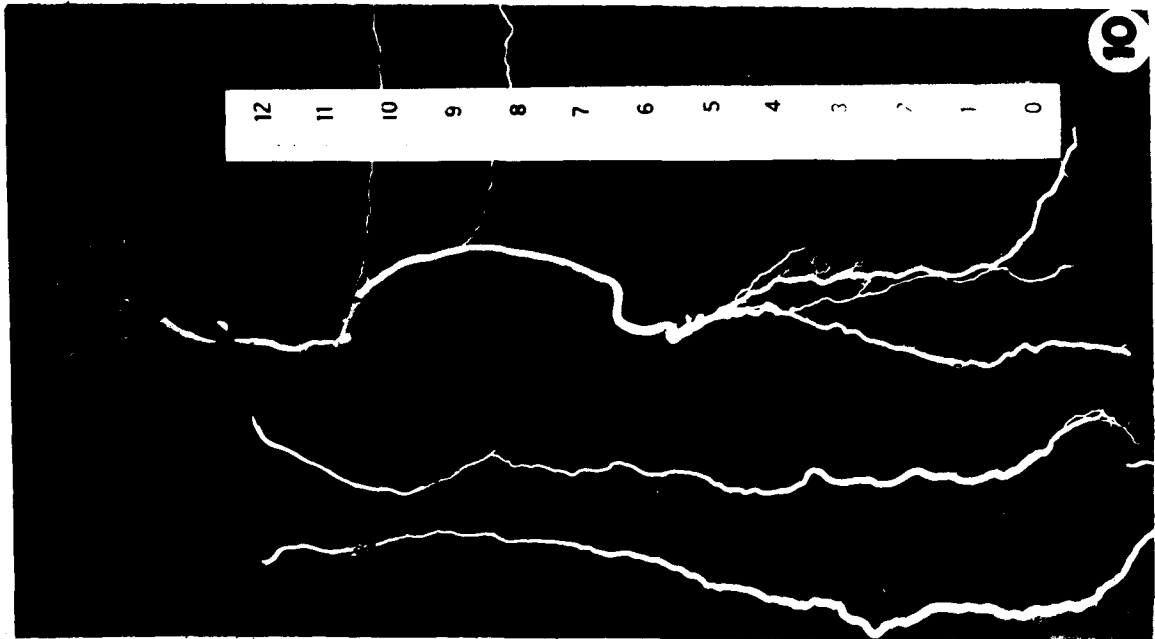
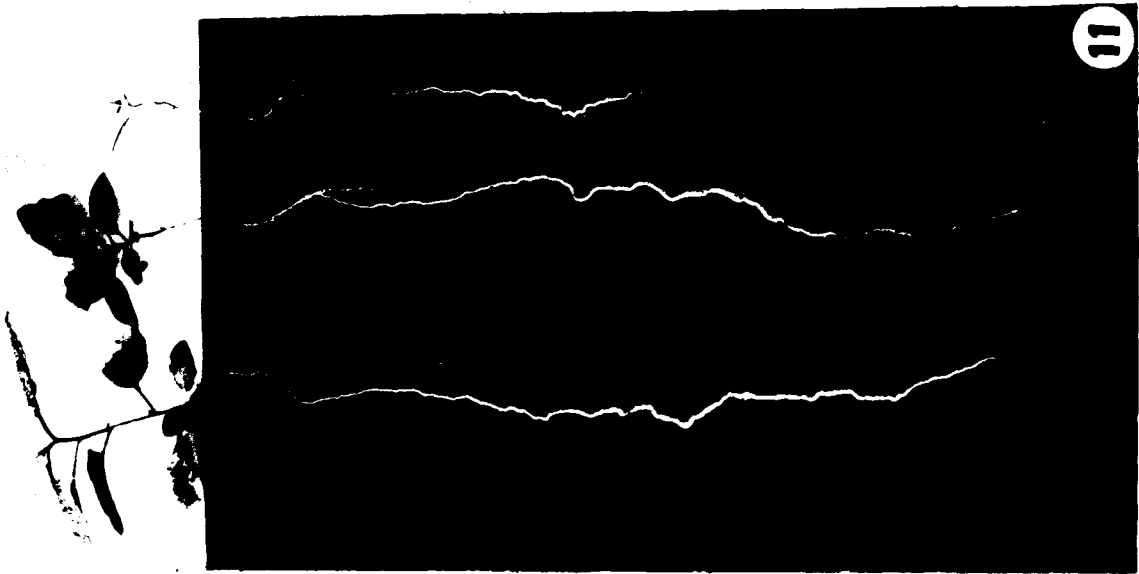
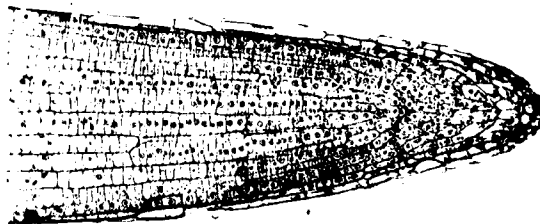
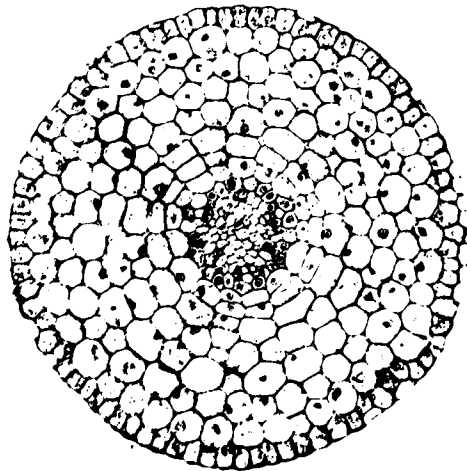
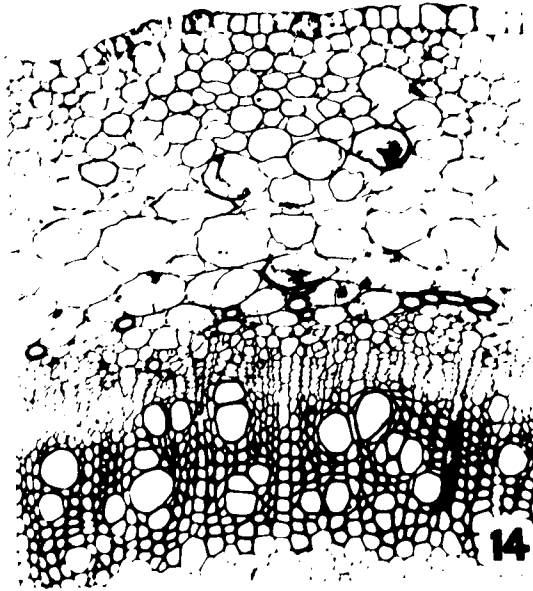


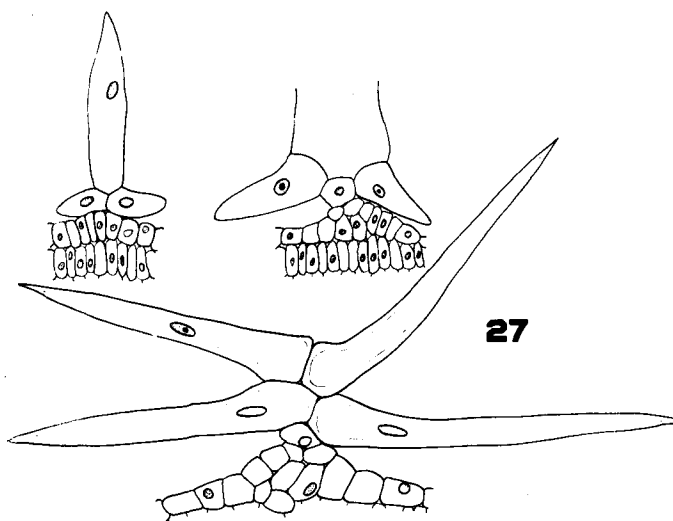
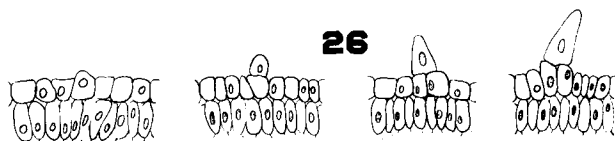
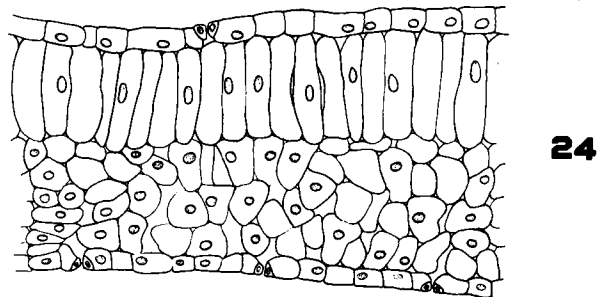
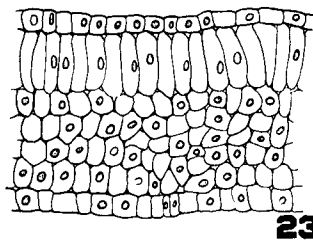
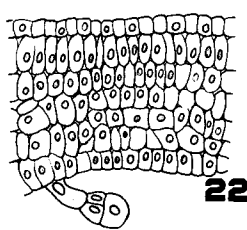
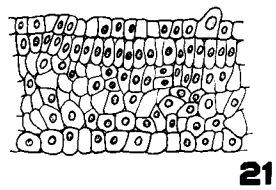
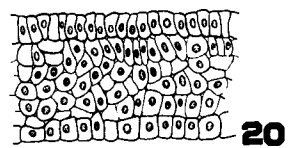
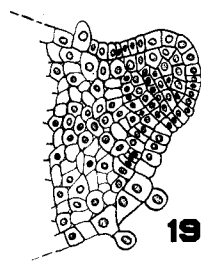
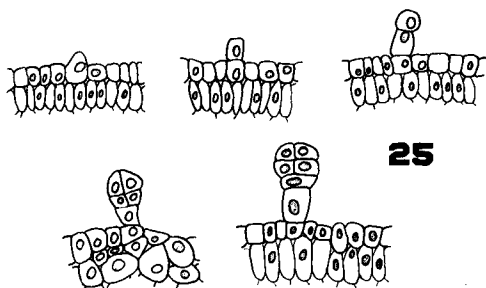
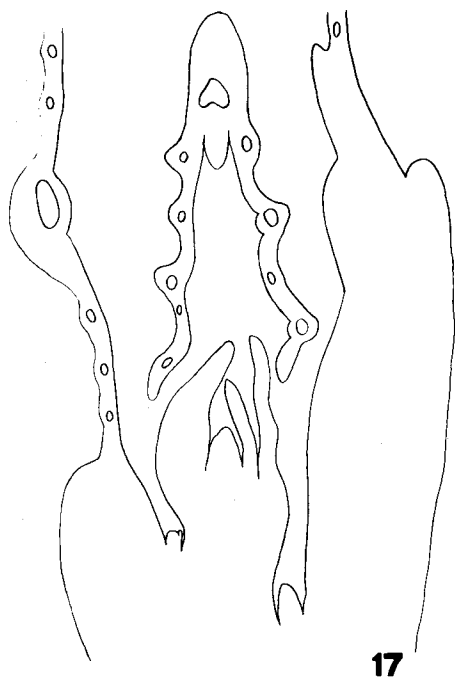
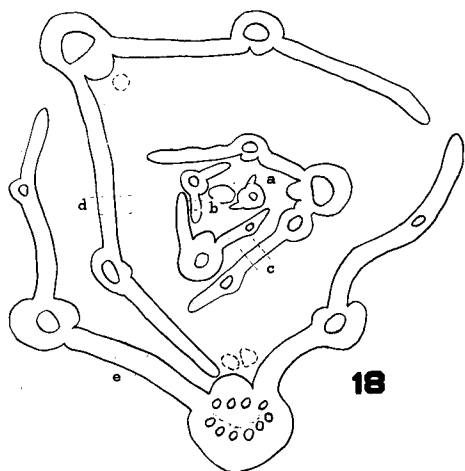
Fig. 14. Cross section of mature stem of horse nettle.

Fig. 15. Cross section of young root.

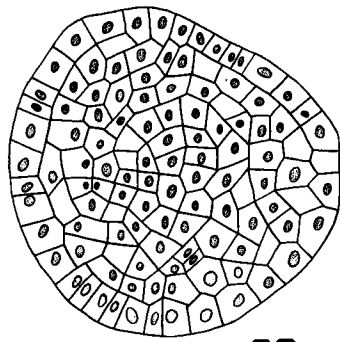
Fig. 16. Longitudinal section of young root tip.



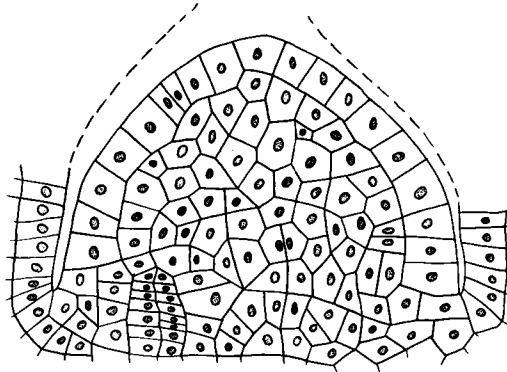
- Fig. 17. Longitudinal section of terminal bud showing growing point, young leaves, vascular strands and axillary buds (x 66)
- Fig. 18. Cross section of bud showing growing point, arrangement of leaves, vascular strands, and axillary buds (x 20)
- Fig. 19. Section of edge of young leaf, corresponding to region "a" of Fig. 18, showing active marginal meristem, formation of hairs, and early stratification of layers. (x 213)
- Fig. 20. Section of young leaf, corresponding to region "b" of Fig. 18, showing isodiametric character of cells, and definite demarcation of upper and lower epidermis. (x 213)
- Fig. 21. Section of young leaf, corresponding to region "c" of Fig. 18, showing definite demarcation and characterization of palisade layer and formation of epidermal hairs. (x 213)
- Fig. 22. Section of young leaf corresponding to region "d" of Fig. 18, showing continued enlargement and differentiation of cell layers, and fully developed capitate hair. (x213)
- Fig. 23. Section of young leaf, corresponding to region "e" of Fig. 18, showing well developed palisade tissue, and lack of conspicuous intercellular spaces in the spongy parenchyma. (x 213)
- Fig. 24. Section mature leaf showing well developed upper and lower epidermis, nearly mature, stomata, and abundant intercellular spaces. (x 213)
- Fig. 25. Five stages in the development of capitate hairs. (x 213)
- Fig. 26. Four early stages in the development of stellate hairs. (x 213)
- Fig. 27. Three late stages in the development of stellate hairs. (x 213)



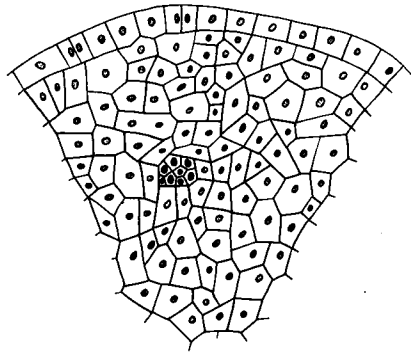
- Fig. 28. Transverse section, histogens of stem apex showing tunica and corpus 80 u from tip. (x 66)
- Fig. 29. Longitudinal section, histogens of stem apex showing tunica, corpus and initiation of procambial strand. (x 66)
- Fig. 30. Transverse section, initiation of procambial strand, 130 u from tip. (x 66)
- Fig. 31. Increase in size of procambial strand 150 u from tip. (x 66)
- Fig. 32. Initiation of cambiform activity and interfascicular cambium. (x 66)
- Fig. 33. Mature stem a = epidermis, b = chlorenchyma, c = collenchyma, d = cortical parenchyma (x 66).
- Fig. 34. Mature stem a = cortical parenchyma, b = endodermis, c = phloem parenchyma, d = companion cell, e = sieve plate, f = cambium, g = xylem, h = pith, i = sieve plate of inner phloem.



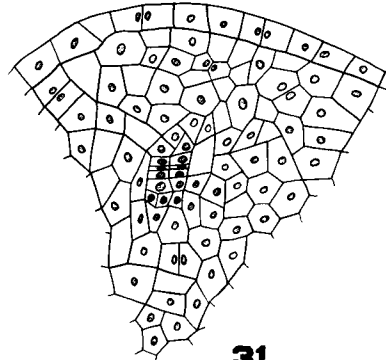
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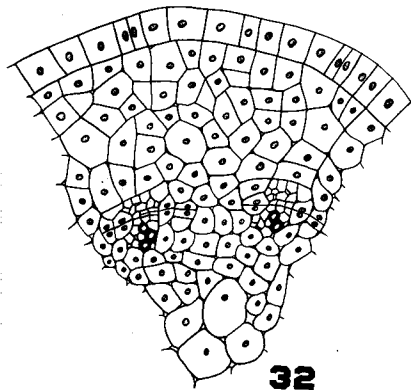
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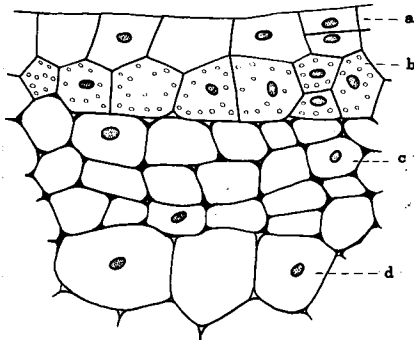
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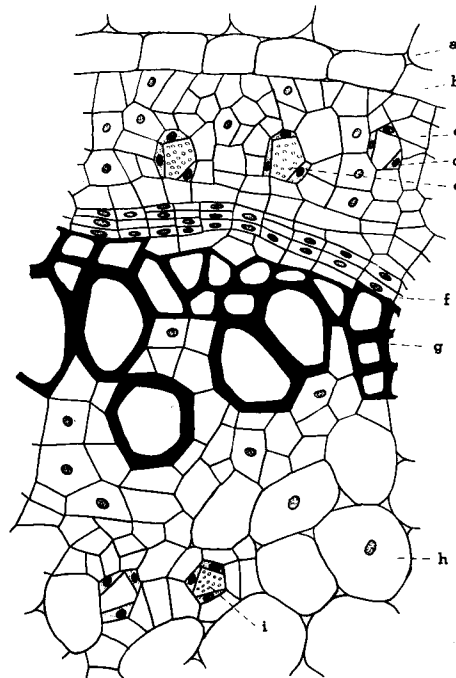
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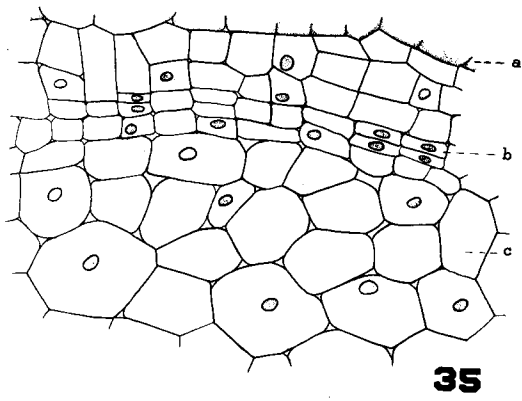


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- Fig. 35. Periderm of mature root, a = remains of sloughed cortical cells, b = periderm, c = cortical parenchyma (x 213).
- Fig. 36. Mature root, a = cortical parenchyma (secondary phloem), b = cambium, c = xylem vessels, d = tracheids, e = xylem parenchyma (x 213)
- Fig. 37. Floral primordium, flattening of apex. (x 63)
- Fig. 38-42. Initiation and growth of calyx primordia. (x 63)
- Fig. 43. Initiation of corolla. (x 63)
- Fig. 44. Arching of calyx and corolla. Initiation of stamens. (x 63)
- Fig. 45. Continued growth of calyx, corolla, and adnate stamens. Initiation of carpels. (x 63)
- Fig. 46, 47. Continued growth of all floral parts. (x 63)
- Fig. 48. Completion of unfolding of carpels. (x 63)



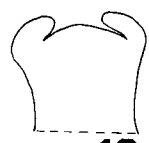
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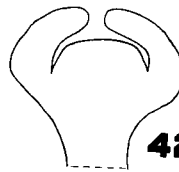
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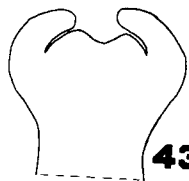
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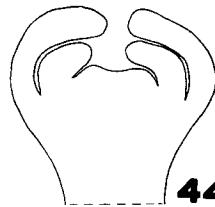
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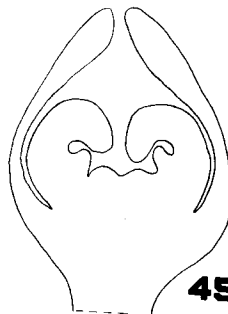
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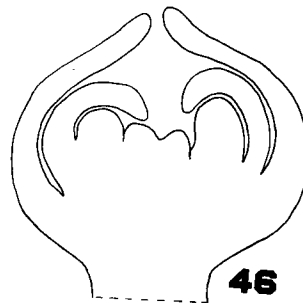
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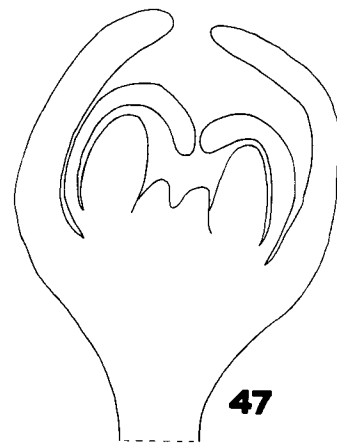
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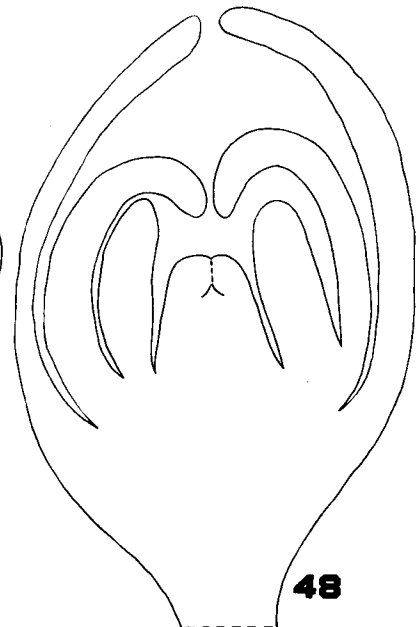
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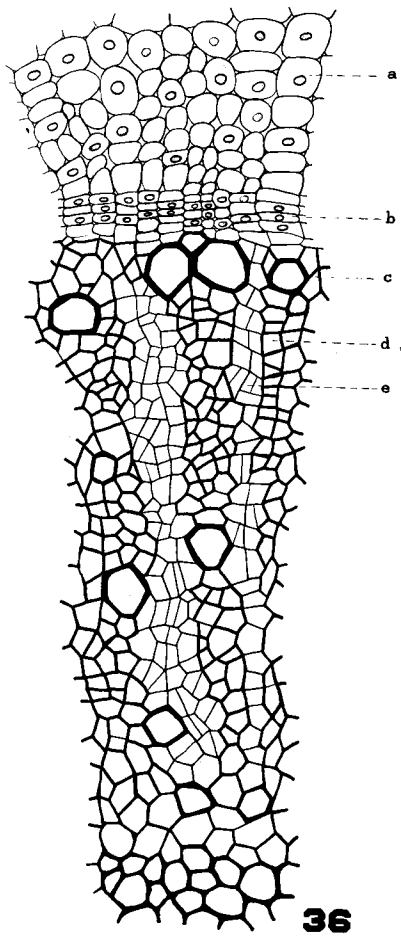
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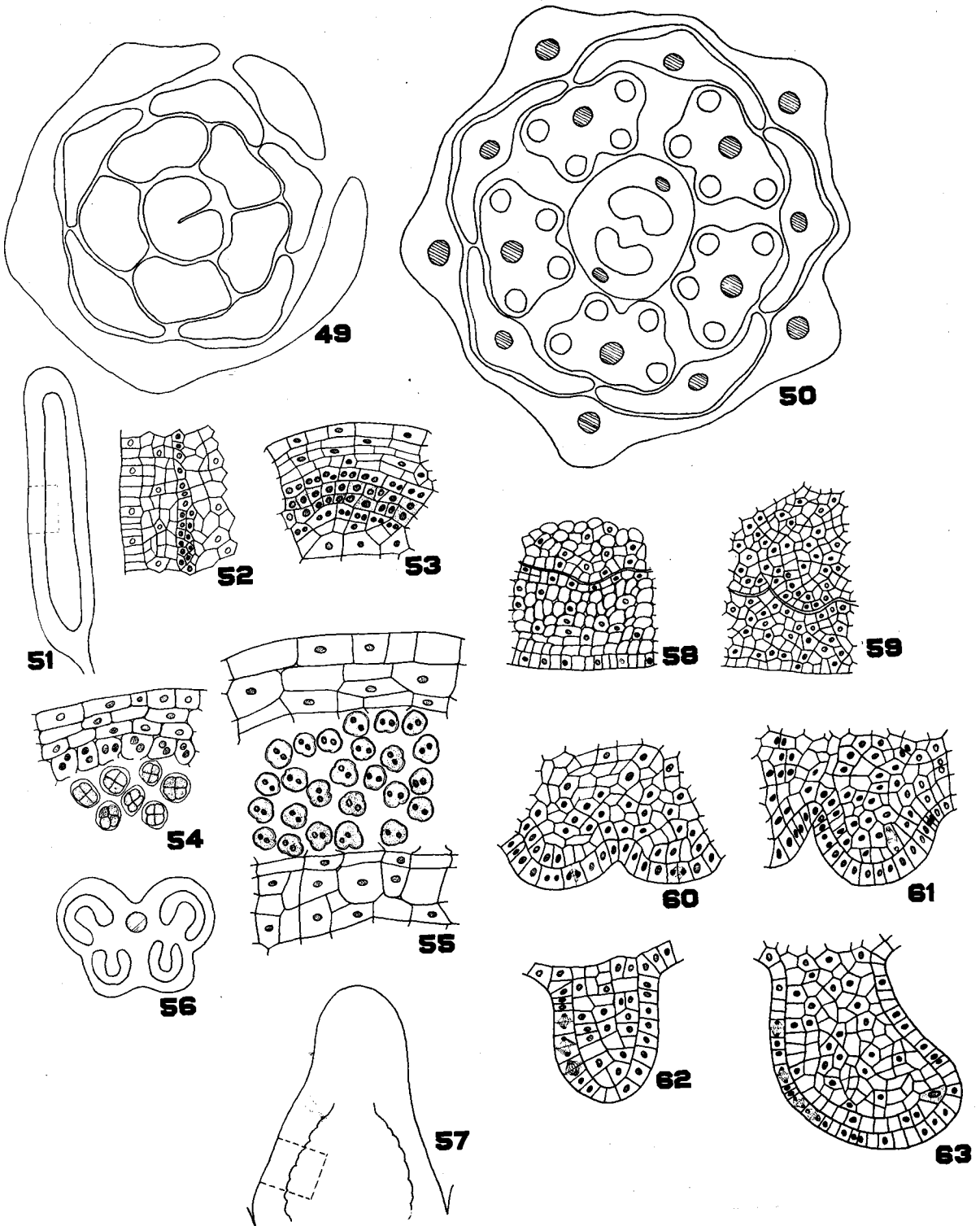
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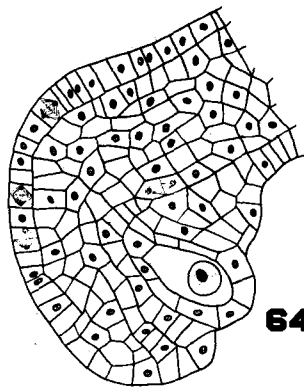
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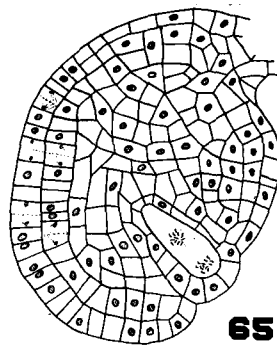
- Fig. 49. Cross section of young flower (x63)
- Fig. 50. Cross section of mature flower (x63)
- Fig. 51. Longitudinal section of anther showing archesporial region (x 63)
- Fig. 52. Young archesporium from region depicted in Fig. 51 (x 213)
- Fig. 53. Transverse section of young archesporium (x426)
- Fig. 54. Pollen tetrad (x426)
- Fig. 55. Mature binucleate pollen grains showing exine and intine (x426)
- Fig. 56. Mature anther showing arc shaped archesporia (x33)
- Fig. 57. Young ovary showing region of young ovule primordia (x63)
- Fig. 58. Cross section of ovary showing beginning of ovule formation (x213)
- Fig. 59-62. Continued development of ovules (x426)
- Fig. 63. Beginning of curvature of ovule and differentiation of megasporocyte (x426)



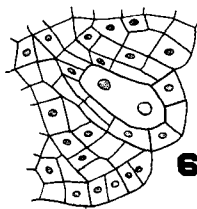
- Fig. 64. Sporocyte previous to first division. Anticlininal division of ovule cell results in Anatropous ovule. (x426)
- Fig. 65. First (reduction) division in sporocyte. (x426)
- Fig. 66. Binucleate stage following first division. (x426)
- Fig. 67. Second division of meiosis. (x426)
- Fig. 68. Linear megaspores. (x426)
- Fig. 69. Disintegration of three megaspore. (x426)
- Fig. 70. Enlarged functional megaspore. (x426)
- Fig. 71. Mature embryo sac showing egg cell, synergids, polar nuclei and antipodals. (x426)
- Fig. 72. Fertilized egg (xygote). (x426)
- Fig. 73. Two celled proembryo. (x426)
- Fig. 74. Four celled proembryo. (x426)
- Fig. 75. Eight celled proembryo. (x426)
- Fig. 76. Multi celled proembryo. (x426)
- Fig. 77. Multi celled proembryo showing (a) dermatogen (b) plerome initials (c) periblem initials (d) suspensor cell (x426)
- Fig. 78. Mature embryo showing (a) cotyledons (b) plumular growing point and (c) radicle.



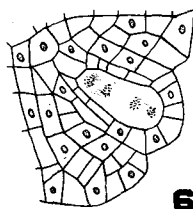
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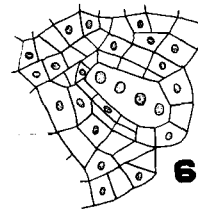
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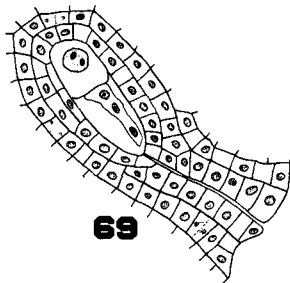
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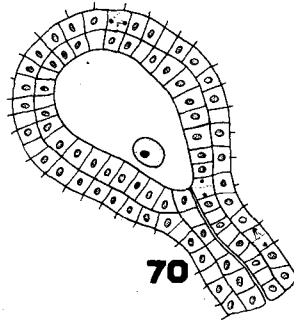
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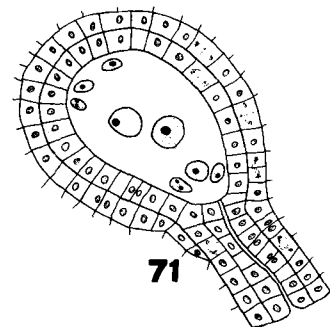
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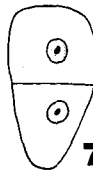
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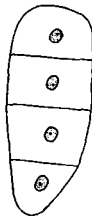
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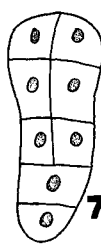
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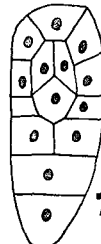
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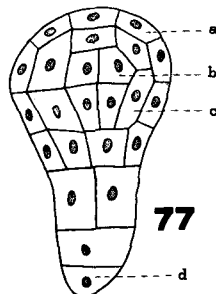
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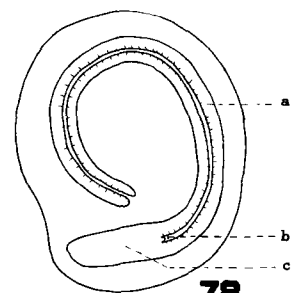
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